Ecology of frontier populations of the invasive grey squirrel (*Sciurus carolinensis*) in Ireland

Emily A. Goldstein MSc, BA

This thesis is presented to the National University of Ireland, Cork, in candidature for the degree of Doctor of Philosophy

Research supervisors:
Dr Fidelma Butler
Dr Colin Lawton

School of Biological, Earth and Environmental Sciences, College of Science, Engineering and Food Science, University College Cork

Head of School: Professor John O'Halloran

May 2014

Abstract

The rise in invasive species, together with habitat destruction, is associated with worldwide declines in biodiversity and ecosystem functioning. Management and control of invasive species, as well as amelioration of invasion impacts, provide unending challenges to species and ecosystem ecologists as well as conservation managers. All continents and many islands have experienced species invasions, often accompanied by severe and long-lasting ecological and economic costs.

Although any species can become invasive if it is transported to, establishes in and spreads in a new environment outside of its native range, rodents are a particularly frequent invader. Rodent introductions are often inadvertent but are also commonly intentional as these animals are traded and transported as pets and may escape from captivity. Tree squirrel species are attractive to humans and are able to establish populations with only a few founding individuals, making them a group well suited to performing the role of biological invaders. The eastern grey squirrel (*Sciurus carolinensis*) is the most commonly introduced squirrel species worldwide.

This research addressed the grey squirrel invasion and frontier population biology. Novel results were generated through diverse research techniques. Public squirrel sighting surveys and hair-tube surveys were used to locate the southern frontier of grey squirrel range expansion in Ireland. A 22-month intensive live trapping study of two frontier populations facilitated the collection of personality and demographic data from squirrels in increasing populations. A systematic literature search on grey squirrel demography provided context for the studied populations, among frontier and established introduced populations, as well as those in the native range. Advanced spatially explicit population modeling techniques predicted future uncontrolled range expansion and objectively compared the outcomes of 12 grey squirrel management strategies.

The current southern extent of the grey squirrel was identified during the two-year citizen science survey that was completed in 2012. Hair-tube surveys recorded grey squirrels in four of the 14 study sites, but were not effective in recording the species close to the leading edge of expansion identified in the citizen science survey. During the live trapping work a total of 130 individual grey squirrels were captured on 1,072 occasions over 3,880 trap days in two frontier sites. Simple measures of personality provided a baseline dataset for the species and indicated that personality is driven by both state dependent and individual variation. Population densities were low and breeding rates high in both populations indicating increase. The annual survival rate was estimated at 31.7% ± 4.7 and was not significantly different between the two sites. After controlling for habitat type, the literature search identified trends in demographic parameters that differentiated between frontier and established introduced grey squirrel populations as well as those from the native range. The grey squirrel invasion has caused varying impact levels in different European countries and these were reflected in demographic parameters. Without intensive and coordinated region-wide management or control, the grey squirrel population is predicted to continue to expand to the south and south west of Ireland. Fatal control measures were predicted to have a greater effect on reducing squirrel abundance and slowing expansion than non-fatal immunocontraception control techniques. Habitat modification measures via broadleaf removal or carrying capacity reduction were also predicted to be effective in reducing abundance and slowing range expansion.

The methods and results are discussed in both a basic scientific and applied invasion management context. An improved understanding of the behaviour, population dynamics, and future scenarios at the frontier of species invasions is crucial for managers worldwide and this is provided here for the grey squirrel in Ireland.

Acknowledgements

That I was able to create and present the body of work that follows is due in no small part to the significant support I have received over the last few years and longer. The skills and experience that I have gained through this project have made all the tough times worthwhile. Thank you to everyone whose presence and advice helped me reach the finish line.

Most special thanks, first of all, are due to my supervisors, Colin Lawton and Fidelma Butler. I learned so much from both of you over the last few years about the whole research process from design, techniques, analysis, writing, and about being a scientist in general. Colin, you taught me to not take myself so seriously, how to think positively and how to turn problems into solutions. Fidelma, you taught me to think creatively and to always question what I thought I knew. You both guided me through the system masterfully and were great role models. Thank you both for your experience and stories.

The Irish Research Council funded the majority of this project. Thanks are due for additional funding from UCC School of BEES, NUIG Department of Zoology and COFORD. Thanks to Coillte, for permission to carry out fieldwork on their properties. Thanks to Marie Roche for excellent Coillte crop maps. I wouldn't have gotten far without the UCC technical staff. Special thanks to Luke Harman for the sturdy construction of hair tubes and squirrel traps, Stuart Warner for GIS genius, and Allan Whitaker for facilitating the vehicles. Thanks also to John Quinn, a brilliant scientist and teacher, for his interest and collaboration. Warm thanks to Pádraig "Pat" Whelan for his support.

Special thanks go to my "big squirrel sister", Emma Sheehy, the one who went before me. You are an inspiring scientist and you taught me so much over the last few years. Thank you for being there and for all the advice you generously shared. Thanks to Amy Haigh for advice on innumerable topics. To my officemates in the ERI: Tad, Eugene, Rosalyn, Maria, Fabio, Erin, Marion, and Roz. And thanks to

Margaret in NUIG, your turn is next! Fieldwork was made easier and more enjoyable by the presence of many: especially Aisling (fieldwork champion), Tad, Eugene, Darragh, Amy and Erin. Huge appreciation goes to the OPW tour staff (Patricia, Mary, Margaret and Karen) at the Swiss Cottage in Cahir and the caretaker Ollie (for emergency trap repair skills). Margaret, thank you for letting me stay with you while trapping. Karen, I always enjoyed the days you were out with me the most! I am grateful to the other postgrads in UCC, especially Megan, and colleagues in the ERI for distraction, commiseration, and especially all of the tips and tricks.

I owe a great debt to my first scientific mentors, Gary Gillis and Stan Rachootin, professors at Mount Holyoke College, MA. Gary, you first showed me how to critically read a scientific paper, what research actually was, how to suture and how to make a killer Powerpoint presentation. Stan, you showed me the beauty in the natural world and the depth and breadth of your knowledge is awe-inspiring. Thank you for knowing I was destined for squirrels long before I did, and for the generous gift of Monica Shorten's "Squirrels" as I left MHC in 2007.

Thanks, with love and affection, to the rodents who have passed through my life. To Pepper, Salty, Pete and Lance – the chinchillas that started my interest in rodents. Special thanks to Jerry the degu, my constant companion these last few years.

I have nothing but unending thanks and gratitude for both of my parents for their constant support (emotional, financial and otherwise) and belief in my ability to accomplish anything. You placed the utmost value on education, always pushed me to do my best and taught me that it's always worth working a little bit harder. This thesis is my tribute to you. Grateful thanks to my younger brother, David, for constant encouragement, humour, and the generous offer to search Yale's electronic library for those hard to access PDFs.

And finally, my ultimate thanks go to Vince Murphy. You encouraged me the whole way along and helped in more ways than I could ever list. Thank you from the bottom of my heart and know that this wouldn't have happened without you.

Declaration

This thesis has not been submitted, in whole or in part, to this or any other university in candidature for any other degree and is, except where otherwise stated, the original work of the author.

Chapter 2, except where otherwise stated, has been accepted in its current form by *Wildlife Research* (doi: 10.1071/WR13197). The author list is as follows: Goldstein EA, Lawton C, Sheehy E, Butler F.

Input of each author to chapter 2:
Author 1: Experimental design, all field and laboratory work, all analysis, and all writing except for the following:
Author 3: Design of the citizen science questionnaire and website.
Authors 2 & 4: Supervisory role.
At least three anonymous reviewers provided helpful input during three rounds of review.

Personality data collection methodology and analysis for chapter 3 was carried out in collaboration with Dr John L Quinn (School of BEES, UCC), who also had a supervisory role for this chapter.

Signed…….

Date…….

Table of Contents

“An ecological explosion means the enormous increase in numbers of some kind of living organism – it may be an infection virus like influenza, or a bacterium like bubonic plague, or a fungus like that of the potato disease, a green plant like the prickly pear, or an animal like the grey squirrel.” – Charles S. Elton (1958)

Chapter 1 –

Introduction

A grey squirrel in Massachusetts – part of its native range. Photo: Sarah Woodruff

1.1 Biological Invasions

Throughout the history of life on Earth, species have enlarged or contracted their natural ranges in response to *inter alia* changing climate or geological processes. Until the last c. 10,000 years, allopatric species were only brought together as a result of the erosion of mountain ranges, glacial recession, continental drift or other similar landscape altering events. Humans transported and cultivated agricultural plants and animals as societies evolved and people migrated across the globe. As humans intentionally moved domesticated stock and crops they also unintentionally transported commensal species or pests and parasites. In recent times, the rate of introductions of non-native species has drastically escalated alongside the ever-increasing ease and speed of international travel. Biological invasions of France, for example, occurred at a rate of less than one per century between the beginning of the Holocene period and the middle of the European Age of Exploration (9200 BC – 1600 AD) but have now increased to over 136 invasions over the last 50 years; a rate of increase that is reflected across Europe (Pascal *et al.* 2010). Species are now purposely moved to new locations for many reasons including garden landscaping, the pet trade, sport hunting or agriculture or inadvertently during transport of food, products or construction machinery (Hulme *et al.* 2008).

Charles S. Elton was said to have founded the science of biological invasions with his 1958 book "The ecology of invasions by animals and plants". Since the publication of that fundamental work, the discipline of invasion ecology has separated from the rest of ecology and other sub-disciplines, including succession ecology, where overlap in techniques or cited literature would be expected (Davis *et al.* 2001). The field of invasion ecology has also suffered from inconsistency in terminology with words such as invader, coloniser, alien, exotic, non-native *etc.* being used somewhat interchangeably (Figure 1.1; Davis and Thompson (2000)). Encouragingly, authors have responded to calls for focus on the issue and tightened terminology resulting in the number of invasion ecology papers published increasing exponentially since 1990 (Lockwood *et al.* 2007; Richardson and Pyšek 2008). Published work in invasion ecology now focuses on the environmental interactions

and effects of species transported by humans to a novel environment in which they establish, spread, and cause significant impacts to native species or ecosystems.

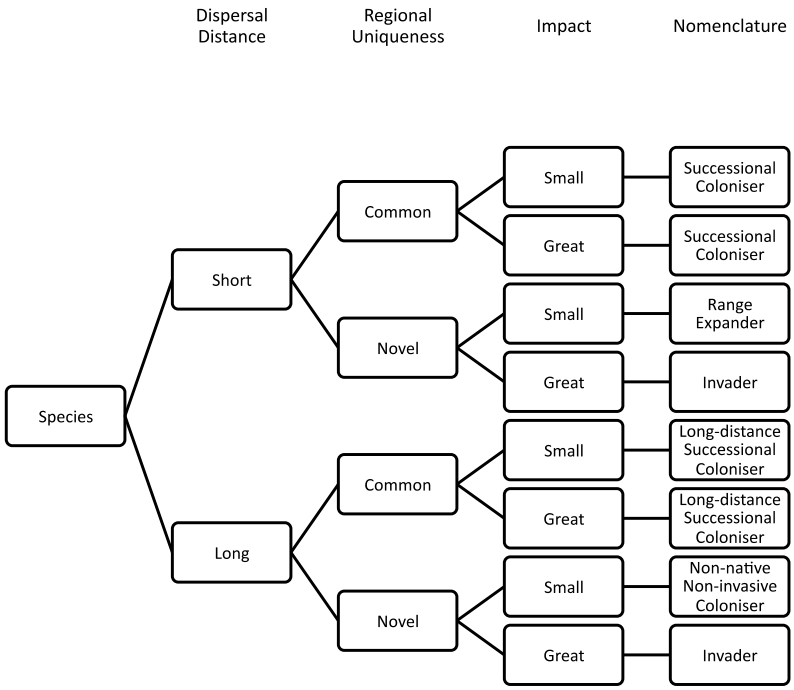


Figure 1.1 Invasive species terminology. Nomenclature scheme to improve consistency in terminology for invasion ecologists adapted from Davis and Thompson (2000).

1.1.1 Stages of Invasion

All biological invasions are fundamentally similar. A successful invader must survive a number of stages or phase transitions (Sakai *et al.* 2001; Kolar and Lodge 2002). There are opportunities at each stage and transition for vigilant landscape managers to apply control measures and achieve the eradication of the species before it becomes established or invasive (Leung *et al.* 2002). Early investigations into the consequences of introduction found that invasion is the least likely outcome with only a small percentage (~10%, i.e. the tens rule) of species transitioning to the

next stage (Williamson and Fitter 1996). While the tens rule appears to be supported by plant species introductions (Boudouresque and Verlaque 2002), recent work suggests that closer to 50% of introduced animals are likely to transition between stages to establish and then spread (Jeschke and Strayer 2005).

Firstly, a species must be transported through human agency from its native area and released in a location outside of its potential natural range. Rapid sea and air travel, along with more hospitable conditions aboard transportation vectors, improve the chances of survival of both intentionally transported species and stowaways. Entry of non-native species can be prohibited by international laws (Mack *et al.* 2000) or reduced by careful treatment of transported material, ballast, and holding containers. Vigilance, quarantines and control at entry points such as seaports or airports may also be effective at reducing arrival of live potential invaders (Mack *et al.* 2000; Lockwood *et al.* 2007).

The second stage of invasion is the establishment of a functioning population in the new range. Successful establishment depends both on the abilities of the potential invader to adapt to its new environment and the susceptibility of that environment to invasion. Ecologists have sought to objectively identify which traits predispose a species to be a good invader with the hope that recognition of these traits will help managers prevent future introductions of species likely to become invasive. Species that are introduced with high propagule pressure, or frequent introductions of large numbers of individuals, are more likely to establish (Kolar and Lodge 2001). In terms of animal introductions, those that successfully establish tend to consist of species that are non-migratory, produce multiple broods per season, and experience a good match between origin and destination habitat (Kolar and Lodge 2001; Forsyth *et al.* 2004). The invasibility of an ecosystem varies over time and for each arriving species (Davis *et al.* 2005). Species-poor communities, such as islands or highly disturbed ecosystems, have been found, in general, to be more invasible as they possess vacant niches that can be readily exploited by an arriving species (Lonsdale 1999; Lockwood *et al.* 2007). Community invasibility can be limited by

preventing vacant niches through reducing anthropogenic disturbance and ensuring the good health of native species communities.

The final stage of invasion is the spatial spread and rapid growth in abundance of established non-native populations. Many researchers have noted that there is a pronounced lag between establishment and significant invasive range expansion (Bertolino *et al.* 2014) during which either exponential growth begins or evolutionary processes are taking place (Sakai *et al.* 2001; Crooks 2005). This lag phase may result in non-natives escaping the notice of authorities while populations become firmly established. Depending on the dispersal abilities of the new invasive, the spread phase can be slow, regular, rapid, or unpredictable. Early models simplified the spatial spread of invasives to a steady and regular progress through the landscape (Skellam 1951; Okubo *et al.* 1989) but recent work has highlighted the importance of long-distance dispersal events and landscape composition in the spread of invasive species (Urban *et al.* 2008; Bled *et al.* 2011). Such studies suggest that many terrestrial species invasions do not progress as a two-dimensional solid front moving uniformly across the landscape (With 2002; Hastings *et al.* 2005), but instead through nodes or foci ahead of the established range which then merge (Moody and Mack 1988; Florance *et al.* 2011). Invaders that show habitat preferences will tend to move unevenly through the landscape following habitat boundaries which can be one-dimensional in the case of riparian specialists such as the invasive American mink (*Neovison vison*) (Fasola et al. 2011). The difficulties involved in representing such a complex expansion process cartographically means that range expansion is still often displayed as an occupied zone with a linear frontier. At this point in the invasion process, eradication is often no longer feasible and control or exclusion become more realistic management options.

1.1.2 Impacts of Invasion

The final quality that differentiates invasive species from expanding non-natives, in the accepted terminology, is that the species causes a negative impact at one or more

levels of the native ecosystem (Davis and Thompson 2000). If the invader and native species are closely related, introgression of genes between the species can occur. Hybridisation results in the dilution of the native genetic resource with the alleles of the invader and can result in effects at the individual or population level. For example, up to 40% of native red deer (*Cervus elaphus*) and invasive sika deer (*C. nippon)* show signs of allelic introgression in zones of overlap in Scotland (Goodman *et al.* 1999). Can or should the red-type deer still be considered a native species in such a case? Other individual level effects of invaders such as reduced native species condition, fitness, or behavioural changes often translate into population level effects on demographic processes such as survival and fecundity rates. The presence of red fire ants (*Solenopsis invicta*) causes behavioural changes associated with fitness consequences in the old field mouse (*Peromyscus polionotus*), in that the mice show stronger aversion to areas with the ants than to areas with indirect or direct predation risks (Orrock and Danielson 2004).

Perhaps arising from the species-centric focus of ecological research, population level effects are the most studied type of invasive species impact (Parker *et al.* 1999). Where native and invasive species compete for resources the survival, reproduction, and/or recruitment rates of the inferior competitor suffer, leading to population declines or range reductions (e.g. Gurnell *et al*. (2004b)). Invasive predators have great scope to impact potentially naïve or vulnerable native species, as is the case when rats or cats predate island birds (Jones *et al.* 2008; Medina *et al.* 2011). Introduced species may also carry disease-causing pathogens or parasites that negatively effect native species; such as squirrelpox virus, which is often fatal to native red squirrels and carried by the invasive grey squirrel (Tompkins *et al.* 2003), or the obligate crayfish parasite *Aphanomyces astaci*, which causes crayfish plague in native European crayfish species where they overlap with invasive American species (Aquiloni *et al.* 2011). Invasive species have the potential to cause harm to native populations through any one or a combination of these impacts. Negative ecological consequences of invasive species can reach even more widely throughout the ecosystem by disrupting trophic cascades and modulating nutrient cycling

systems or disturbance regimes (Vitousek and Walker 1989; D'Antonio and Vitousek 1992; Kimbro *et al.* 2009).

Aside from the serious ecological consequences of invasive species briefly outlined above, invaders often bring with them severe economic costs both through direct damage to human enterprise or costs associated with control. In the United States damage and control costs relating to invading organisms amount to approximately \$120 billion year^{-1} (Pimentel *et al.* 2005). Zebra mussels (*Dreissena polymorpha*) alone, which entered the waterways of the United States through ballast water, cause approximately \$1 billion year^{-1} by biofouling of water pipes and electricity generation plants and associated control costs (Pimentel *et al.* 2005). The economic and ecological impacts of this species will only increase as it is expected to invade freshwater habitats in much of the eastern half of the United States and parts of the west coast (Drake and Bossenbroek 2004). On the island of Ireland direct costs of invasive species are estimated at over €250 million year^{-1} (Kelly *et al.* 2013).

1.2 Motivations for the current research

Biological invasions as a whole are said to be one of the leading drivers of worldwide biodiversity loss (Vitousek *et al.* 1997; Clavero *et al.* 2009) though some question the direct causality of the relationship (Gurevitch and Padilla 2004; Didham *et al.* 2005). Despite the international importance and immediacy of the issue, much remains unknown about the ecology of biological invasions. One of the difficulties of the field is that despite the basic similarities in the process and impacts of invasion events described above, each biological invasion is unique as regards the invading species and the invaded ecosystem. Every invasive species has the potential to cause differing impacts in each environment to which it is introduced. As such, it is difficult and somewhat rare for research on particular invasive species to be relevant, or applicable to other species or the broader field of invasion ecology. Furthermore, conservation managers and policy makers who have an urgent need of clear and concise guidance on biological invasions may find much

of the published literature to be inaccessible, either because of pay-walls and restricted access to journals or jargon-heavy language, or not directly pertinent to specific situations (Leung *et al.* 2005).

Adequate management of a species invasion requires precise and up-to-date knowledge of the location, local ecology of the species, as well as the current and potential future impacts of the species. The accurate characterisation of the frontier zone of an invasion is crucial for conservation managers for the design of landscape management plans and priorities, but is often not a major focus of invasion research (but see Sweetapple *et al*. (2004); Brown *et al*. (2006); Fujisaki *et al*. (2010)). Future invaded range can be extrapolated from sequential species distribution surveys. An ongoing rapid and adaptive monitoring programme alongside an understanding of invasion potential, however, would afford managers the most accurate and up-to-date information on species invasion frontiers and progression through the landscape. Evidence of range expansion or contraction can provide managers with feedback on the necessity or effectiveness of control measures planned or undertaken.

Further studies, in more taxa, are needed to understand how and why individuals composing frontier populations may or may not be fundamentally different, in form or behaviour, to those in established populations. For example, cane toads (*Bufo marinus*) on the invasion frontier in Australia exhibit different movement behaviours, in that they move further, more often, and in straighter trajectories, and were shown experimentally to have greater endurance than toads in established populations (Llewelyn *et al.* 2010). It has been suggested that successful invasive animal species tend to be behaviourally flexible and generalist, able to overcome challenges at each phase of invasion and progress to the next (Sih *et al.* 2012). Founder populations in some species have been found to be composed of more bold or aggressive dispersive individuals than those in long-established populations (Dingemanse *et al.* 2003; Rehage and Sih 2004; Duckworth and Badyaev 2007). It may be shown in the future that differences in personality or behavioural type between frontier and established invasive populations lead to varying effectiveness

of management actions. If this proves to be the case, conservation managers will require a thorough understanding of how population personality composition changes with time since invasion.

Insights into the functioning of frontier populations could lead to better predictions of future expansion and invasion impacts or inform practical control strategies. Different types and levels of impacts could manifest according to time since population colonisation and whether invader density is increasing or holding steady. The control of invasive species, especially invasive mammals, is often a contentious issue between certain public interest groups and scientists (Bertolino and Genovesi 2003), a situation that is likely not improved by the tendency of invasion biologists to use subjective and militaristic language (e.g. invasion, eradication, novel weapons, explosion, front, tactical control, etc.) crafted to attract attention of editors, funding bodies and the media when communicating and publishing results (Larson 2005). Objective comparisons of control programmes and methodologies ahead of implementation could serve to reduce conflict over such decisions and lead to greater consensus on the proposed action as well as ultimately produce a more successful response to the biological invader.

Better understanding of frontier population ecology can only be gained through basic research. The importance of frontier population characteristics was identified in an early spatially explicit population modeling paper:

> "It is possible that the values given for grey squirrel mortality and fecundity by Gurnell (1987), represent measures determined from studies of established populations rather than those at the boundary of an invasion front. Populations of grey squirrels at the edge of an invasion front are likely to experience different conditions to those of an established population in that population densities will be low and probably subject to less intraspecific competition" (Rushton *et al.* 1997).

Though couched in the confident language of scientific writing, these sentences reveal the substantial assumptions that the authors made when modeling the

expansion of grey squirrels in the north of England. Assumptions highlight areas of the field that would benefit from future focused research.

1.3 Approach and Aims

Scientific research does not move forward in isolation; it takes small steps forward informed by previous work. To this end, this thesis research was undertaken within the context of a well-studied mammalian invasive species in a well-studied landscape. The ecology of grey squirrels (*Sciurus carolinensis* Gmelin 1788) in their native range is well known (Gurnell 1987; Koprowski 1994; Steele and Koprowski 2001; Thorington Jr *et al.* 2012). The grey squirrel is included in a list of some of the world's worst invasive species (Lowe *et al.* 2000) and is the subject of what is considered to be one of the best studied biological invasions (Gurnell *et al.* 2006). The invasion has been thoroughly studied in Britain and Italy where many research groups have focused on diverse aspects of the invasion including, but not limited to, interactions with the native red squirrel (Gurnell *et al.* 2004b; Wauters *et al.* 2005), long term population trends (Gurnell 1996), spatially explicit population modeling (Rushton *et al.* 1997; Lurz *et al.* 2001; Tattoni *et al.* 2006), and bark stripping impacts (Kenward and Parish 1986; Mayle *et al.* 2009). The grey squirrel in Ireland is also well studied and the distribution (O'Teangana 1999), vagility (McGoldrick 2011), response to control measures (Lawton 1999), and predator-prey interactions (Sheehy 2013) of this species have been the subject of post-graduate work and several peer-reviewed publications (e.g. O'Teangana *et al.* (2000a); O'Teangana *et al*. (2000b); Lawton and Rochford (2007); McGoldrick and Rochford (2009); Sheehy and Lawton (2014)). All previous work on grey squirrels in Ireland has been carried out on established populations and advanced modeling techniques have not yet been applied to the system.

Ample opportunity therefore existed for further novel research on the grey squirrel invasion in Ireland informed by existing knowledge of the species and the body of data relating to its presence in Ireland. The southern expansion frontier of the

species was known to be advancing (Carey *et al.* 2007) and was therefore an ideal location to investigate the ecology and dynamics of grey squirrels in frontier populations. The underpinning aim of this thesis was to examine multiple facets of populations at the frontier of an invasion, in order that conservation and management responses to biological invasions might be better informed and more effective. The thesis is presented as a series of self-contained chapters written in paper style. Chapter 2 presents the first comparison and evaluation of the cost-effectiveness and ability of simple citizen science surveys and traditional hair-tube surveys to locate an invasion frontier and is now an accepted manuscript (Goldstein *et al.* 2014). A short section composed of additional methodology and discussion, which was not relevant for publication, follows the main body of the chapter. Chapter 3 examines personality in two frontier grey squirrel populations and considers the influence of state-dependent and individual variation on personality expression. Chapter 4 investigates the demographic and vital statistics of two frontier grey squirrel populations and places the findings in the context of demographic trends from other frontier and established introduced populations and populations within the native range. Chapter 5 presents a validated, transparent, and carefully calibrated spatially explicit population model of the grey squirrel invasion of the Irish landscape to make predictions of future range expansion and objectively compares the outcome of several potential control strategies. Chapter 6 presents a synthesis of the themes running through the results of this research and recommendations for further research and future invasive grey squirrel management.

Chapter 2 –

Locating species range frontiers: a cost and efficiency comparison of citizen science and hair-tube survey methods for use in tracking an invasive squirrel.

A baited and set squirrel trap in Cahir Park, Co. Tipperary, Ireland

This chapter has been accepted in its current form and published:
Goldstein EA, Lawton C, Sheehy E, Butler F. 2014. Locating species range frontiers: a cost and efficiency comparison of citizen science and hair-tube survey methods for use in tracking an invasive squirrel. Wildlife Research 41(1): 64-75.

Abstract

Context. Improved knowledge of changing species distributions is critically important for conservation managers in the face of increasing species invasions, habitat disturbance and climate change. Efficient monitoring of the location of advancing species invasion frontiers is especially crucial for effective species community and habitat management.

Aims. To compare the cost-effectiveness and efficiency of two survey methods, a citizen science survey and a traditional hair-tube survey in their abilities to locate the current southern invasion frontier of grey squirrels (*Sciurus carolinensis*) in Ireland.

Methods. In the citizen science survey we collected sighting reports of the grey squirrel and its native congener, the red squirrel (*S. vulgaris*), from the geographic region of the invasion frontier from untrained members of the public over a two-year period. Hair-tube surveys were carried out in 14 woodlands (≥ 30 hectares) in the same geographic area to test the ability of this indirect field method to identify colonizing grey squirrel populations. The costs, efficiency, and cost-effectiveness, of each method were compared.

Key results. The citizen science sighting reports resulted in the clear delineation of the southern frontier of the grey squirrel invaded zone. The hair-tube survey ascertained the presence of grey squirrels in four of 14 sites but did not detect this species close to the invasion frontier defined by the citizen science survey. Though the total cost of the citizen science survey was higher it was more cost-effective and efficient on a per detection basis for the purposes of detecting the presence of grey and red squirrels.

Conclusions. The citizen science survey detected invasive squirrels in sites where the hair-tube survey did not. As such, the citizen science survey provided a more comprehensive snapshot of the location of the grey squirrel invasion frontier more efficiently and cost-effectively than traditional field techniques.

Implications. In the face of increasing ecological and economic costs of biological invasions, we recommend straightforward citizen science surveys, over indirect field

surveys, to managers and researchers seeking to efficiently track progressing invasions of readily-observable animals cost-effectively.

2.1 Introduction

The ecology of invasive species and invaded ecosystems is a well-published and sometimes controversial topic in the larger fields of ecology research (Mack *et al.* 2000; Davis *et al.* 2001), applied landscape management, and public policy (Lodge and Shrader-Frechette 2003). When invasive species advance through exclusion barriers and control measures are unsuccessful, longer term monitoring and management becomes necessary (Bertolino and Genovesi 2003; Courchamp *et al.* 2003; Simberloff 2003). It is difficult for landscape managers with limited resources to maintain surveillance on occupied areas while also tracking the advancing or evolving frontier and managing damage caused by the invader. As such, decisions on invasive species monitoring techniques should be taken transparently with careful consideration given to the most effective use of available budgetary and time resources without unnecessary sacrifice of scientific rigor (Gaidet-Drapier *et al.* 2006; Tulloch *et al.* 2011). Authors have argued the need for more research into choosing efficient and effective methods for monitoring species distribution, richness, and the change in these metrics over time (Barea-Azcón *et al.* 2007; Lyra-Jorge *et al.* 2008). A cost-effective survey method is one that provides the highest rate of return or greatest benefit (e.g. in terms of species detectability or number of species detected etc.) for a given level of investment. Previous studies have compared the efficiency and cost-effectiveness of numerous direct and indirect field survey methods in determining species presence and/or abundance (Gurnell *et al.* 2004a; Gaidet-Drapier *et al.* 2006; Garden *et al.* 2007; Lyra-Jorge *et al.* 2008; Roberts 2011; Tulloch *et al.* 2011; Paull *et al.* 2012). However, invasive species tracking is a particularly challenging case due to the potentially rapid spread of a species through the landscape. As a result, there is an urgent need in the invasive species management and research fields for novel methods to keep up with the frontier of spread. Here we compare the efficiency and efficacy of a field survey method with an alternative citizen science approach for locating the invasion frontier of a spreading introduced species.

Citizen science is an increasingly well-utilised tool in species richness and distribution studies. It has been suggested that ecological studies that span large national and international areas require an element of citizen science (Cooper *et al.* 2007; Cohn 2008; Silvertown 2009; Devictor *et al.* 2010). While the employment of species sightings reports from the public in scientific endeavors is not novel, the utilization of lay people for more complex and involved surveys has greatly increased in the last decade as have the project design strategies and statistical methods involved in obtaining optimal, least-biased results (Tulloch and Szabo 2012; Tulloch *et al.* 2013a; Tulloch *et al.* 2013b). Publicly-collected datasets, which have the capacity to monitor biodiversity over space and time or from sometimes inaccessible privately-owned lands (Dickinson *et al.* 2010), are a boon to species distribution science. Dickinson *et al*. (2010) note that the public can be particularly effective at recording the presence of species that are rarely seen or have low population densities and are therefore an asset in tracking the expanding ranges of invading species or wildlife disease (Eraud *et al.* 2007; Koenig *et al.* 2007; Peacock *et al.* 2007; Delaney *et al.* 2008; Fujisaki *et al.* 2010).

Indirect field surveys for the presence of animal species have the benefit of being cost-effective, time-efficient, requiring little need for the licencing or training of operators, and causing little stress to the animal being surveyed in comparison to direct capture trapping surveys. Evidence of species presence in an indirect survey is gathered through the collection of a visual sighting or physical sign left behind by the species, which may be subject to identification uncertainty. Examples of indirect species presence surveys include sighting transects, point observations, feeding transects, scent stations, scat surveys, drey counts, footprint tunnels, and the use of remote wildlife camera traps (Brown *et al.* 1996; Barea-Azcón *et al.* 2007; Gurnell *et al.* 2009). A further method, the hair-tube or hair-snare survey, is a widely used type of indirect survey that allows for the methodical collection of small mammal hair in order to establish presence in a site (Scotts and Craig 1988; Catling *et al.* 1997; Pocock and Jennings 2006; Harris and Nicol 2010; Schwingel and Norment 2010; Reiners *et al.* 2011). Though less intensive than direct capture surveys, the downside of hair-tube surveys is that they can still be expensive in personnel time

and equipment costs, and therefore there are trade-offs in the area that can be covered compared with the ability to detect a species.

The eastern grey squirrel (*Sciurus carolinensis*), native to eastern North America, has been frequently introduced to locations worldwide (Bertolino 2009) where it often easily establishes (Wood *et al.* 2007) to the detriment of native sciurid populations (Kenward and Holm 1993; Gurnell *et al.* 2004b; Sainsbury *et al.* 2008). The grey squirrel was introduced to one site in the Republic of Ireland in 1911 (Watt 1923; O'Teangana *et al.* 2000a), via populations in Great Britain (Figure 2.1). Since then the range of the grey squirrel has expanded to the north, east and south of the island of Ireland, resulting in a corresponding decline in the population and range of its native congener, the Eurasian red squirrel (*S. vulgaris*) (Wauters *et al.* 2000; Carey *et al.* 2007; Lawton *et al.* 2010). The landscape in Ireland is primarily agricultural though forest cover has recently exceeded 10% and, though patchy, is increasing. Approximately 62% of Ireland's human population is concentrated in urban areas while the remaining 38% is well distributed throughout the rural landscape, which covers 97.6% of the total Irish land area (CSO 2011).

We chose the two squirrel species present in Ireland to test the cost-effectiveness and efficiency of citizen science and indirect field surveys in determining invaded range as both species are charismatic, relatively easy to distinguish from one another and rare in certain areas. The grey squirrel invasion and the 'plight of the Irish red squirrel' are well and emotively covered in national news media and nature television programming resulting in a public that is reasonably aware of the situation of these species. Hair-tube surveys have proved a reliable technique in Ireland to record the presence of both red and grey squirrels (Finnegan *et al.* 2007; Waters and Lawton 2011; O'Meara *et al.* 2012) and were utilized in detecting the presence of these species elsewhere in Europe and North America (Gurnell *et al.* 2004a; Fimbel and Freed 2008; Bertolino *et al.* 2009; Bertolino *et al.* 2014). In the present study we apply both methods: 1) a citizen science survey for squirrel sightings and 2) a hair-tube survey for squirrel presence, along the southward invasion frontier of the grey squirrel. We compare the strengths and weaknesses as well as the overall costs, cost-

effectiveness and efficiency of both methods in acquiring species detection records and characterizing the advancing edge of the invasive squirrel population. We discuss the fitness of each method for the stated purpose and make recommendations for their use in future research or management projects.

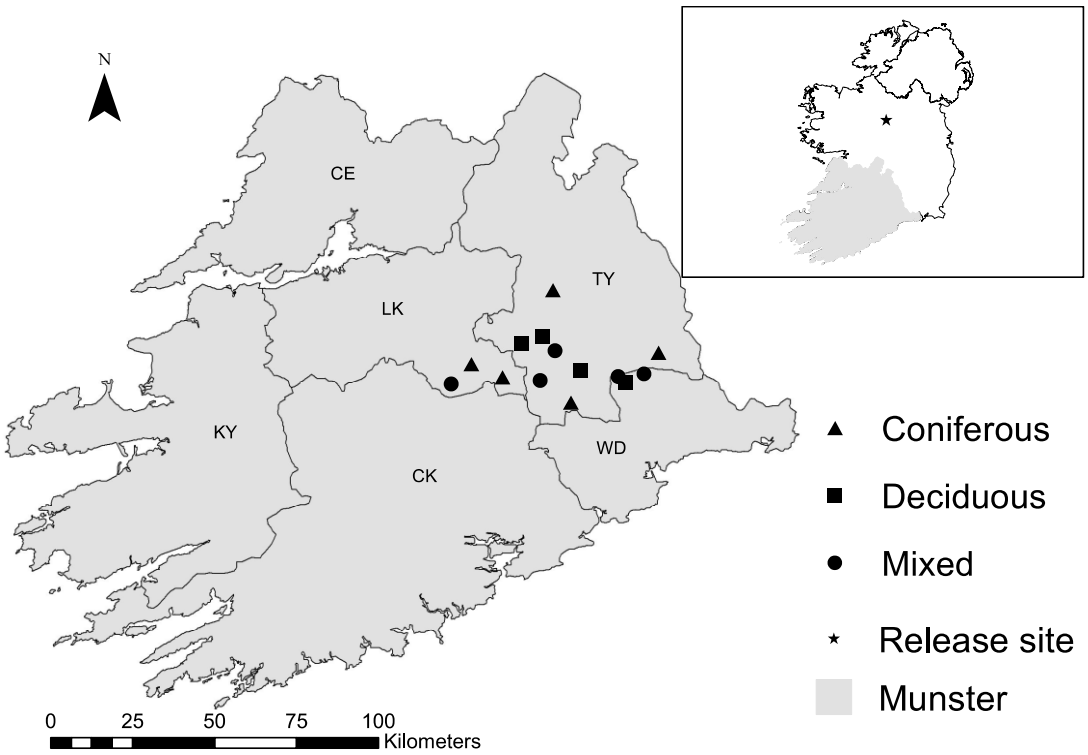


Figure 2.1 Map of Munster Province showing the location and habitat types of the 14 hair-tubes surveys for the presence of *Sciurus carolinensis* and *S. vulgaris*. Habitat types of the survey sites are indicated by symbol shape; (filled triangle) coniferous habitat, (filled square) deciduous habitat, (filled circle) mixed habitat. Inset map of the island of Ireland displays the extent of Munster Province and the initial release location of *S. carolinensis* (star). County abbreviations: CE (Clare), CK (Cork), KY (Kerry), LK (Limerick), TY (Tipperary), and WD (Waterford).

2.2 Materials and methods

2.2.1 Citizen science survey

We collected records of red and grey squirrel sightings from the public in Munster Province, Republic of Ireland (2011 human population: 1,246,088 (CSO 2011)) which includes the previously determined southern invasion frontier of the grey squirrel (Carey *et al.* 2007) (Fig. 2.1). To reduce the possible bias of the urban/rural divide of the human population on sighting distribution we employed diverse methods to publicise the survey over the course of the study in an attempt to reach all potential groups of volunteers. Sightings were solicited between November 2010 and October 2012 and publicity was sustained throughout that period through: a dedicated website; colour posters distributed to notice boards in local population centers; presentations to the public; articles in local and national newspapers, as well as continuing local and national radio and television coverage. Background information pertaining to both species of squirrel was provided with each public mention of the survey project. We did not request volunteers to report sightings from specified areas or seek reports of species absence. Volunteers reported their sightings either through the website facility, by telephone or post. Respondents provided the species, date and location of the sighting, habitat type, condition of the animal (live/road kill etc.) and contact information. Sighting reports were accepted when the respondent indicated the sighting was of a deceased specimen, provided photographic evidence, or if the respondent, upon interview, was able to adequately describe the species sighted. Sighting reports that did not fulfill the above criteria or did not include sufficient contact information to allow for follow-up were not incorporated into the analysis or results. The survey responses from the six Munster counties of Clare, Cork, Kerry, Limerick, Tipperary, and Waterford were mapped in ArcMAP 10 (ESRI). Sighting reports within 1 km of each other, the maximum distance a squirrel will normally travel within its range (Gurnell 1987), were grouped to avoid duplication and over-sampling.

2.2.2 Hair-tube survey

Indirect field surveys using hair-tubes to record the presence of squirrel species were initiated in 14 woodlands in Munster between March and August 2011 (Figure 2.1). All sites were ≥ 30 hectares (ha) and were classified as one of three forest types: coniferous (≥80% conifer coverage; n=5), deciduous (≤25% conifer coverage; n=4), or mixed woodland (n=5). Survey sites were chosen *a priori* on the basis of available and accessible forested habitat and proximity to the previously published southern extent of grey squirrel range (Carey *et al.* 2007).

The hair-tubes consisted of 300 mm lengths of 65 mm x 65 mm square PVC pipe (Gurnell *et al.* 2004a; Finnegan *et al.* 2007). The tubes were tied to trees at a height of approximately 1.8 m and baited with whole hazelnuts and a 4:1 whole maize and shelled peanut mixture. Two removable wooden blocks, each with three 10 mm x 10 mm squares of paper-backed adhesive, were positioned with metal clips on the inside upper surface at either end of each tube to collect mammalian dorsal hairs. Thirty hair-tubes were set out in each site at a density of 1 tube ha^{-1} for a period of 14 days (Finnegan *et al.* 2007; Bertolino *et al.* 2009; Gurnell *et al.* 2009) after which they were retrieved, cleaned and redeployed with fresh glue blocks in a new site.

Collected mammal hairs were removed from the glue block with forceps and cleaned with distilled water and a histological clearing agent (Histo-Clear, National Diagnostics, Hessle Hull, UK) to remove oil. Hairs (≤ 10) from each positive tube were arranged on separate gelatin-coated microscope slides using the techniques described in Teerink (1991) to create impressions of the cuticle scales. The distinctive scale patterns on the hair shield, viewed with 100x magnification under a light microscope, allowed for identification of hair collected in each tube to the species or genus level. We viewed cross-sections of *Sciurus* hair shields under 100x magnification by cutting each perpendicularly with a razor blade and fixing it to the side edge of a microscope slide in order to differentiate grey squirrel (oval) from red squirrel (concavo-convex) hair (Teerink 1991).

2.2.3 Cost-effectiveness analysis

Accurate calculation of the cost-effectiveness and efficiency of a survey method requires an estimation of the research or conservation value of the data collected by each survey method and a calculation of the costs. We utilised multiple metrics in our analysis including number of locations where squirrels were detected (unique detections) and how quickly these reports were obtained, detection efficiency (detections day^{-1}), and spatial detection efficiency (detections ha^{-1}), as well as the cost-effectiveness metric of cost per detection (cost $detection^{-1}$). Cost-effectiveness metrics divide the realised scientific benefit by the cost required to achieve it. The cost of each survey method was calculated based on the cost output required to detect squirrel species presence at each location and the total cost to complete each survey. We divided costs into four main areas of expenditure for each survey method: equipment/one-off costs, bait/consumables costs, personnel costs, and travel costs (Garden *et al.* 2007). A summary of prices and costs is given in 2012 Euro (Table 2.1; see Appendix 1 for details of expenditure).

Equipment/one-off costs encompassed expenses related to acquiring the materials necessary to complete the survey but were not consumed completely during the course of the study. Hidden costs not taken into account in the equipment cost calculations were the light microscope used to identify mammal hairs and the ArcGIS10 licence fee. Bait/consumables costs covered expenditures on bait for the hair-tubes and materials that were consumed during laboratory and citizen science publicity work. Personnel costs were calculated at three rates depending on the hourly wage of the person(s) required to complete each task. The majority of the tasks could have been assigned to a basic level research assistant employed at the rate of €12.50 hr^{-1} but others required the expertise of a technical officer (€25.00 hr^{-1}) or an IT professional (€30.00 hr^{-1}). Travel costs were calculated based on the mileage cost of €0.39 km^{-1} charged for the hire of institutional vehicles.

A comparison of the detection or non-detection of squirrels within the 14 hair-tube sites with detection in the entire region encompassed by the citizen science survey is

not sufficient on its own for the objectives of this research. For the direct comparison of survey methods, the set of sighting reports from the citizen science survey only included those originating from locations within the hair-tube study sites and during the five-month period over which hair-tube surveys were performed. We calculated the overall and standardised cost-effectiveness (detections $cost^{-1}$) and spatial cost-effectiveness (detections $cost^{-1}$ ha^{-1}) of both survey methods. A higher cost-effectiveness value is indicative of a wiser resource investment.

Table 2.1 Costs by category of the hair-tube survey, both total and per survey, and the citizen science survey, total and per week, to detect squirrel presence.

Where appropriate costs are separated by initial outlay or per survey/week. Personnel time for the hair-tube survey included fieldwork and laboratory analysis but refers to publicity, website and data management for the citizen science survey. Additional detail on costs is provided in Appendix 1.

		Initial outlay (€)	*Price per survey/week (€)*	*Total (€)*
Hair-Tube Survey	Personnel	425.00	525.00	7775.00
	Travel		143.52	2009.28
	Equipment	300.55		300.55
	Bait/Consumables	108.82	3.78	161.74
Total		**834.37**	**672.30**	**10246.57**
Citizen Science Survey	Personnel	1459.92	108.04	12279.92
	Travel	448.50		448.50
	Equipment		1.37	142.00
	Bait/Consumables	60.00		60.00
Total		**1968.42**	**109.40**	**12930.42**

2.2.4 Statistical analysis

The number of hair-tubes containing red squirrel hair, the number containing grey squirrel hair, and the aggregate number of tubes with hair of either species were expressed as a proportion of the total number of tubes collected in each site. These data were arcsine square-root transformed and the assumption of normality was tested using Levene's test of homogeneity prior to analysis. We performed ANOVA

tests on transformed data to examine differences in the proportion of hair-tubes positive for squirrel hair among site habitat types, and the difference in the proportion of tubes positive for red or grey squirrel hair among habitat types in the four sites where both species were known to be present (Carey's Castle, Bansha, Gortarush and Kilnamack). A 2x3 Fisher's exact test of independence was used to investigate the association of the three habitat types and number of hair-tubes used by each of the two squirrel species (Kirkman 1996). Seasonal effects on the proportion of positive tubes were examined with separate ANOVA tests for each squirrel species using the month collected as a fixed effect. Normality and ANOVA tests were performed using SPSS v. 20.0 (Armonk, NY: IBM Corp.)

2.3 Results

2.3.1 Citizen science survey

During the survey period 665 public reports of squirrel sightings were accepted relating to 424 unique locations in Munster Province from 529 individual members of the public. There was an initial peak in responses following the launch of the survey, though reports were consistently returned throughout the study period for both squirrel species. An accumulation curve reveals that reports from over half of the unique grey squirrel sighting locations were received within the first six months of the citizen science survey (Figure 2.2) after which the speed of report collection slowed at a different pace for each species. We observed that multiple sightings per unique location were generally associated with areas of higher human population density or designated outdoor recreation areas and were not meaningfully linked to the grey squirrel invasion frontier. The majority of locations related to sightings of red squirrels only (n=310), while locations with grey squirrel sightings only (n=62) or sightings of both species in a single location (n=52) were less common (Figure 2.3). We report a conservative estimate of the grey squirrel invaded zone, which incorporates all accepted sightings of grey squirrels in Munster (Figure 2.3). The frontier line is composed of 18 grey squirrel sighting locations. Approximately 90% of these sightings (n=16) had been received by August 2011, 10 months after the

beginning of the citizen science survey. The general shape and location of the frontier was established by sighting locations collected by May 2011, only seven months after the commencement of the survey, by which time 14 of the frontier sightings had been received.

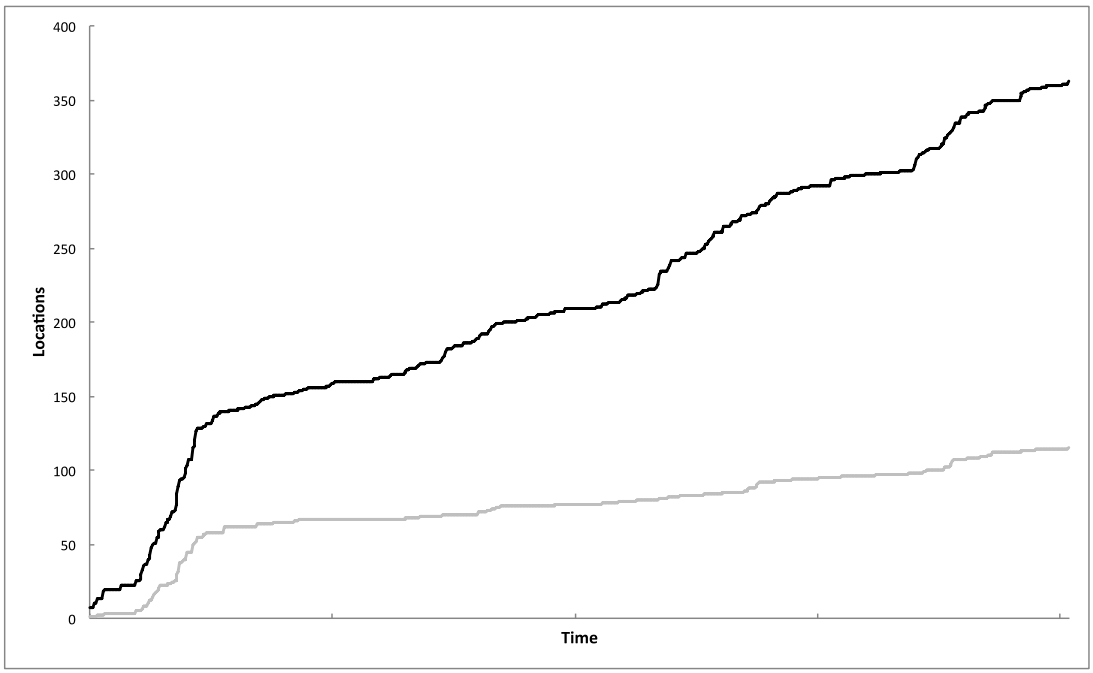


Figure 2.2 Accumulation curve of unique sighting locations for *Sciurus carolinensis* (grey line) and *S. vulgaris* (black line) during the citizen science survey in Munster Province, Ireland. Tick marks on the horizontal axis delineate six-month intervals. The initial peak in number of responses accounted for over 50% of grey squirrel and over 40% of red squirrel locations.

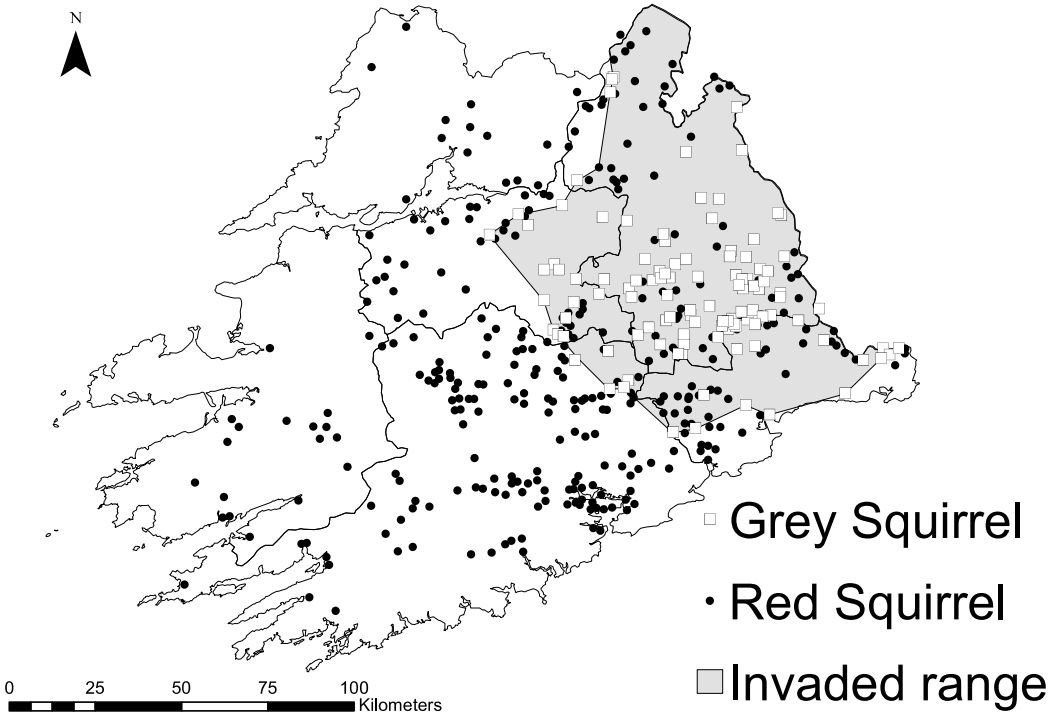


Figure 2.3. Map of Munster Province displaying the locations of public sightings of: *Sciurus carolinensis* (open square), and *S. vulgaris* (filled circle) collected between November 2010 and October 2012 in the citizen science survey. The grey squirrel invaded zone, as determined by the citizen science survey, is shown in shaded grey.

2.3.2 Hair-tube survey

A total of 420 hair-tubes were set out during the course of the 14 surveys of which 184 (43.8%) contained mammal hair, 89 (21.2%) contained bird feathers, and 3 (0.7%) were vandalised or stolen and not included in the analysis. The hairs of seven non-target mammal species were collected in the hair-tubes in addition to the two target squirrel species (Table 2.2). Red squirrel presence was detected in 12 out of the 14 sites surveyed while grey squirrel presence was detected in four field sites only. Grey squirrels were observed during fieldwork in two sites (Carey's Castle and Tikincor) where the presence of this species was unrecorded by the hair-tubes. No collected hair-tubes contained the hair of more than one mammal species.

Table 2.2 Number of sites and hair-tubes within which mammal species were detected at 14 hair-tube study sites in Munster Province, Republic of Ireland.

Additional tubes recorded the presence of birds or were vandalised/stolen. In total 14 sites were surveyed with 420 hair-tubes.

Species	Sites	Hair-tubes
Sciurus carolinensis	4	4
Sciurus vulgaris	12	63
Apodemus sylvaticus	14	75
Crocidura russula	1	1
Mustela erminea	2	7
Martes martes	2	3
Mus musculus	2	2
Myodes glareolus	7	8
Rattus norvegicus	10	21
Bird	12	89
Vandalised/stolen	1	3

Habitat type did not have a significant effect on the aggregated proportion of all hair-tubes visited by squirrels, both red and grey, in each site ($F_{2,11} = 1.059$, $P = 0.380$). Fisher's exact test of independence also found no significant difference in the frequency of hair-tubes positive for either red or grey squirrels among the three habitat types ($P = 0.094$). Grey squirrel hair was detected in three of the four sites where the presence of both squirrel species was confirmed (Table 2.3), however, there was no significant difference between the proportion of hair-tubes positive for red squirrel hair or for grey squirrel hair ($F_{1,6} = 5.188$, $P = 0.063$) in these sites. Neither was habitat type a significant influence on the proportion of tubes visited by either squirrel species (habitat*species: $F_{1,4} = 2.649$, $P = 0.202$), in the four both-species sites. There were no significant time of year effects on the proportion of positive hair-tubes for either species (grey squirrel: $F_{5,8} = 1.448$, $P = 0.305$; red squirrel: $F_{5,8} = 2.407$, $P = 0.129$.)

Table 2.3 Results of the hair-tube and citizen science survey to detect presence of the invading grey squirrel in 14 Munster woodland sites.

Hair-tube results are given as the proportion of tubes used by each squirrel species in each site. C = conifer, M = mixed conifer and deciduous, D = deciduous. The asterisk indicates grey squirrels were observed in the site but not detected by the hair-tube equipment. Red and grey squirrel citizen science sighting reports at the site are indicated by R and G respectively, -- indicates no reports received from the defined area. The citizen science survey return from Gortarush was received outside of the standardised time period, in which the two survey methods were directly compared, and is shown in parentheses.

Site	*Habitat*	*Month collected*	*Proportion tubes used*		*Citizen science survey returns*
			Red	*Grey*	*At site*
Anglesborough	C	May	0.30	0	--
Kildanoge	C	Mar.	0.17	0	--
Killeen	C	May	0.13	0	--
Killurney	C	July	0.10	0	R
Gortarush	C	July	0.21	0.03	(R, G)
Ballydavid	M	June	0.50	0	R, G
Ballyhoura	M	June	0.33	0	R, G
Glengarra	M	Mar.	0.13	0	R, G
Tikincor	M	July	0	0*	R, G
Kilnamack	M	Aug.	0.03	0.03	R, G
Bansha	D	July	0.07	0.03	R, G
Carey's Castle	D	June	0.11	0*	R
Cahir Park	D	Apr.	0	0.03	G
Gortavoher	D	Apr.	0.03	0	R, G

2.3.3 Cost-effectiveness and efficiency of survey methods

The total cost of surveying the 14 sites with hair-tubes was €10,246.57 whereas the citizen science survey cost €12,930.42 over two years in Munster Province (Table 2.1). Personnel time was the most expensive cost category of both survey methods. The initial outlay for the hair-tube study (construction and purchase of field equipment, purchase of bulk materials) made up €834.37 of the total budget while the cost to survey and analyse each of the 14 sites (personnel time, travel, bait) totaled €672.30. The initial outlay (website design and creation, publicity, travel) for the citizen science survey was €1,968.42 and cost a further €109.40 per week to maintain and host the website as well as manage sighting reports. The cost of the

citizen science survey, when standardised to a time period comparable to the duration of the hair-tube survey, was €2850.77.

The restricted set of citizen science sighting reports, used in the calculation of standardised cost–effectiveness metrics, consisted of 10 squirrel sighting locations within the hair-tube study sites. This group of sightings recorded the presence of grey squirrels in eight of the hair-tube field sites whereas red squirrels were recorded in nine sites. The standardised citizen science survey detected the presence of grey squirrels at five sites where they were not detected by hair-tube surveys (Table 2.3). Conversely the standardised citizen science survey did not detect red squirrels at three sites where hair-tubes recorded the presence of this species.

We used the standardised cost of the citizen science survey to compare the cost of each detection of squirrel presence recorded at the hair-tube sites by both survey methods. Comparisons of scientific benefits, efficiency and cost-effectiveness are summarised in Table 2.4. The cost of each detection was considerably lower in the standardised citizen science survey than in the hair-tube study. The cost to detect grey squirrel presence in a site using hair-tubes was also considerably higher than the cost to detect red squirrel presence using the same method. The detection efficiency of the total citizen science programme was higher than the efficiency of the hair-tube survey, though results from the standardised citizen science survey were more comparable within each species. We found that both the total and standardised citizen science survey were more cost-effective than the hair-tube survey programme. The standardised spatial cost-effectiveness of the citizen science survey was also higher than that of the hair-tube survey. Furthermore, though the area covered by the total citizen science survey programme was over 3,600 times larger than the area encompassed by the hair-tube survey, its spatial cost-effectiveness was only lower by two orders of magnitude.

Table 2.4 Summary table of efficiency metrics from citizen science and hair-tube surveys for grey and red squirrels in Munster.

Total programme results relate to the entirety of both surveys. The standardised results were calculated using citizen science records collected over an area and time comparable to the hair-tube survey.

Scale	Efficiency Metric	Citizen Science Survey		Hair-tube Survey	
		Grey Squirrel	Red Squirrel	Grey Squirrel	Red Squirrel
Total Programme	Total area covered by programme (km^2)	15166	15166	4.2	4.2
	Total time covered by programme (days)	730	730	196	196
	Total unique detections	114	362	4	12
	Total cost (€)	12930.42	12930.42	10246.57	10246.57
	Cost-effectiveness of entire programme (detections / cost (€)	8.8×10^{-3}	2.8×10^{-2}	3.9×10^{-4}	1.2×10^{-3}
	Spatial cost-effectiveness (Detections / (cost (€) × ha))	5.8×10^{-9}	1.8×10^{-8}	9.3×10^{-7}	2.8×10^{-6}
	Detection efficiency (detections / day)	0.16	0.50	0.02	0.06
Standardised to field survey area and duration	Total unique detections within area	8	9	4	12
	Standardised cost (€)	2850.77	2850.77	10246.57	10246.57
	Cost per detection (Cost (€) / detections)	356.34	316.75	2561.64	853.88
	Relative cost-effectiveness (detections / cost (€))	2.8×10^{-3}	3.2×10^{-3}	3.9×10^{-4}	1.2×10^{-3}
	Relative spatial cost-effectiveness (Detections / (cost (€) × ha))	6.7×10^{-6}	7.5×10^{-6}	9.3×10^{-7}	2.8×10^{-6}
	Relative detection efficiency (detections / (day × ha))	9.9×10^{-5}	1.1×10^{-4}	4.8×10^{-5}	1.5×10^{-4}
	Spatial detection efficiency (detections / ha)	2.1×10^{-2}	2.3×10^{-2}	9.5×10^{-3}	2.9×10^{-2}

2.4 Discussion

A two-year public survey confirmed the widespread distribution of red squirrels in Munster and characterised the advancing invasion of grey squirrels in this region. It is now clear from the results that the southern frontier of the grey squirrel range has progressed in a southwesterly direction since the most recent Irish squirrel distribution survey (Figure 2.4) (Carey *et al.* 2007) at a rate comparable to mean rates of spread for this species previously estimated in Ireland: 1.94 km $year^{-1}$ (O'Teangana *et al.* 2000a) and 1.75 km $year^{-1}$ (McGoldrick 2011). The favourable comparison between these mean rates of expansion and the current citizen science survey lends credence to the ability of this survey method to accurately track the presence of grey squirrels as the species continues to invade new areas.

As with other volunteer-based citizen science surveys, there was opportunity for biases to affect the quality and evenness of the squirrel sighting data received. Dickinson *et al.* (2010) note that citizen science surveys that do not seek to standardise spatial sampling effort can find an over-sampling of residential, amenity and accessible landscapes and an under-sampling of roadless or inaccessible areas. It is unlikely that this bias would affect the results of the standardised comparison between the two survey methods within the hair-tube sites, and we attempted to control for it within the overall citizen science survey by including only unique sighting locations in the analysis. The hair tube sites were accessible by road and open to the public. On a national scale, Ireland possesses a dense road network for a primarily rural landscape and inaccessible areas are limited. Though we did not find that habitat affected detection of squirrel presence in the hair-tube survey, red and grey squirrels are known to exhibit differing habitat preferences and this may have led to a difference in the capability of the citizen science survey to detect each species. For instance, grey squirrel detection in the citizen science survey may have been enhanced due to this species' well-documented preference for deciduous woodland and ability to thrive in urban or suburban landscapes (Koprowski 1994; Bowers and Breland 1996; O'Teangana *et al.* 2000b), while capacity to perceive the

red squirrel could have been reduced. The red squirrel is known to avoid settling in areas of high human disturbance and is more common in coniferous woodlands (O'Teangana *et al.* 2000b; Bryce *et al.* 2002; Lurz *et al.* 2005), which mostly occur as large plantations away from large settlements in Ireland. A tendency of survey volunteers to preferentially report rarely sighted or unusual species (Galloway *et al.* 2006; Dickinson *et al.* 2010) may have also improved the ability of this survey to detect both species of squirrel due to differing habitat preferences, the recent arrival of grey squirrels, and the more favourable cultural perception of the native red squirrel.

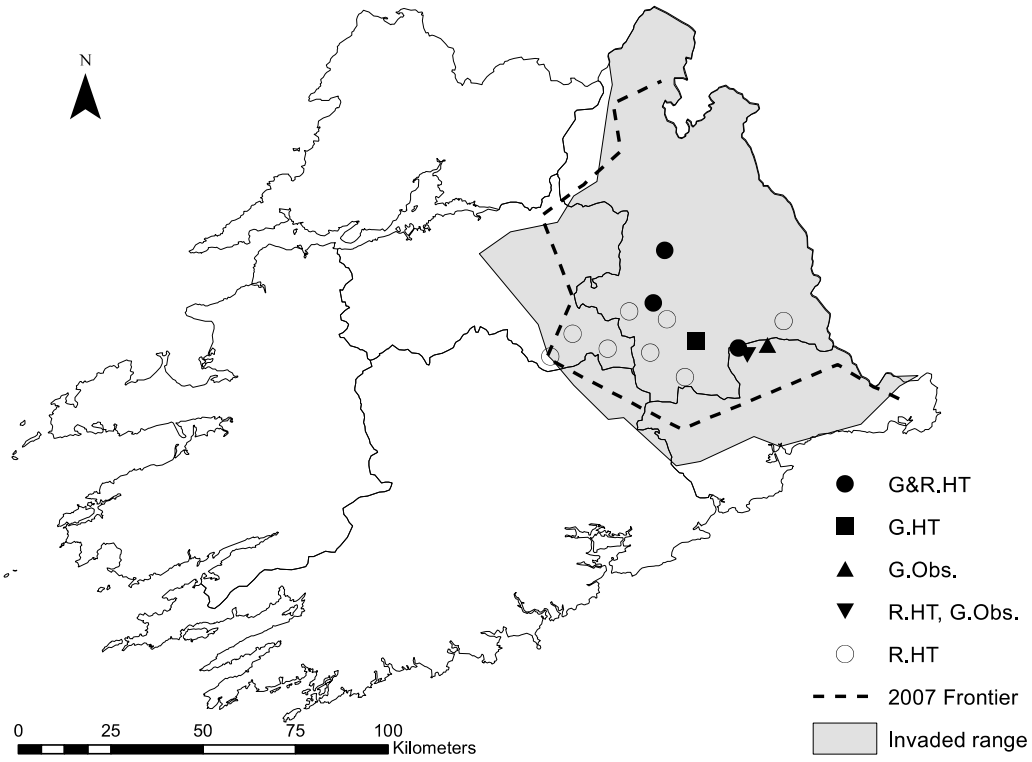


Fig. 4. Squirrel presence detected in Munster Province by the hair-tube survey overlaid on the grey squirrel invaded zone, as determined by the citizen science survey, (shaded grey). The dashed line indicates the identified frontier of the invasive grey squirrel in 2007. The symbols indicate the squirrel presence ascertained at each site; (filled circle) positive for red and grey (G&R.HT), (filled square) positive for grey only (G.HT), (filled triangle) observation of grey (G.Obs.), (filled inverted triangle) positive for red with observation of grey (R.HT, G.Obs.), (open circle) positive for red only (R.HT).

The sighting report acceptance regime was instituted to address a common criticism of previous citizen science projects, namely their reliance on data of unknown quality. The strict sighting acceptance criteria were established to provide a means to distinguish credible sightings from those of uncertain validity. Relevant supplementary information and colour pictures of each species were prominently displayed on the website, posters, and in public presentations to aid identification. We believe the greatest potential for misidentification in this survey is in confusion between red and grey squirrels, rather than misidentification of other mammals as squirrels. Seasonal and age-related pelage colour changes in both red and grey squirrels could deceive inexperienced observers (Shorten 1954; Gurnell *et al.* 2008b), though there are noticeable and easily recognizable differences in the body size and profile of the two species year round. The high number of responses (n=665) from the small geographic area examined should act to reduce the background noise of erroneously accepted sighting reports. Correct species identification and accuracy in location reporting are key issues that researchers overseeing citizen science projects are seeking to address with new tools (Newman *et al.* 2012). For example, research groups are beginning to take advantage of the wide availability of smartphones with GPS technology and state-of-the-art cameras as well as reasonable smartphone application development costs to enhance the spatial accuracy and species or individual recognition capabilities of public sightings (Bolger *et al.* 2012; Teacher *et al.* 2013).

Probability of detection of target species by the survey method is a central consideration when determining species presence with direct or indirect surveys (MacKenzie 2005; Stanley and Royle 2005). False absences, or the non-detection of species that are actually present, are likely to be recorded if the detection probability of members of a population is less than 1 (MacKenzie *et al.* 2002). Numerical estimations of detection probability require repeated sampling occasions at a number of sites. Non-detection of species that are present by the hair-tube surveys may be caused by avoidance of unfamiliar equipment, removal of bait by non-target species, or equipment failure. Red squirrel detection probability with hair-tube surveys has previously been estimated to be relatively high (Mortelliti and Boitani 2008) but can

be affected by habitat type (Amori *et al.* 2012) and detection of non-target species (Mortelliti *et al.* 2010). The detection probability of grey squirrels by hair-tubes has not been similarly examined in the literature and is an area where further study is needed. As each study site was sampled once, it was not possible in the present study to estimate detection probability of the hair-tube surveys directly for red and grey squirrels. However, a comparison of species presence recordings at the 10 sites where citizen science sighting reports spatially co-occurred with the hair-tube surveys illustrates a clear trend (Table 2.3). We have little evidence to suggest that the detection probability of red and grey squirrels by the citizen science survey in the current study is close to 100% (due to citizen scientists not being asked to record absences). However, we have clear evidence that the detection efficiency of the overall citizen science programme is greater than the red squirrel detection efficiency of hair-tubes, which in turn is greater than the grey squirrel detection efficiency of our hair-tube protocol.

Finnegan *et al*. (2007) assert that hair-tube surveys are an effective method to detect grey squirrel presence at low population densities, such as while the species is colonizing new areas. The present study detected grey squirrel presence at distances between 24 and 31 km behind the invasion front defined by the citizen survey (Figure 2.4), which is farther behind the invasion edge than might reasonably be expected if standard 14-day hair-tube surveys were indeed well suited to detecting colonizing populations. While we did not record squirrel density in the hair-tube survey sites to determine whether populations were well established, it must be assumed that these sites were not the most recently colonized because of the measured distance to the edge of the recorded invasion. A limitation of indirect field techniques is that such methods can only detect species presence where deployed and where animals interact with the equipment. Dispersing squirrels may be more difficult to detect with baited equipment because they are transient rather than exploring or foraging and do not remain in the area to become familiar with experimental devices. A recent hair-tube study in an Irish woodland with an established grey squirrel population recorded 20% of hair-tubes positive for grey squirrel (Sheehy and Lawton 2014), which is considerably higher than any

proportion of grey squirrel positive tubes found in the current study. Squirrels in low-density populations may also be less likely to interact with baited equipment due to incomplete exploitation of natural food resources. Habitat type has been shown to influence probability of red squirrel detection by hair-tubes rather than species presence (Amori *et al.* 2012) though in the present study we found no significant effect of habitat on proportion of tubes visited by either squirrel species. Grey squirrels are notably more difficult to live trap in the summer and autumn than red squirrels, during which time they are more attracted to natural food sources than to bait (Perry *et al.* 1977; Gurnell 1996). We did not observe any significant difference in the proportion of tubes visited by either squirrel species due to the spring and summer months (March-August) in which hair-tube surveys were conducted.

The effective recognition of changes in species distribution, abundance and health is critical in all ecosystems in the face of accelerating species invasions, climate change, and increasing anthropogenic disturbance. Often species research or management goals can be convincingly addressed through a combination of complementary survey methods. Long-term and high quality citizen science data sets such as the Christmas Bird Count and the Breeding Bird Survey in North America allow for the monitoring of trends in population size and distribution (Tulloch *et al.* 2013a). Careful examination of these datasets, along with results from other volunteer-dependent surveys such as dead bird reports, has enabled researchers to track the evolving range and influence of the West Nile Virus (LaDeau *et al.* 2007) and compare observed trends with roost surveys or seroprevalence data (Crosbie *et al.* 2008; Wheeler *et al.* 2009). Not all projects need be so far reaching. Indeed, shorter-term localised citizen science projects have provided enhanced insight into species habitat use alongside indirect surveys (van der Merwe *et al.* 2005) and insect biodiversity data in poorly documented habitats (Braschler 2009).

Resource constraints in the conservation management sector dictate that survey methods that are efficient and cost-effective should be the most utilised. While it is

difficult to directly compare the results of a citizen science sighting survey carried out over a period of years with a discrete series of field surveys, we have assessed each method on its cost-effectiveness, efficiency, and ability to detect target species in the geographic area of an invasion frontier. We have shown that more expense was required for each squirrel detection using hair-tube survey techniques compared to our basic volunteer citizen science sighting survey. Indeed, through the overall citizen science programme we were able to collect squirrel species presence information over an area more than 3,600 times as large as the total hair-tube survey area at similar levels of spatial cost-effectiveness. The collection of squirrel presence data over a similar spatial scale with hair-tube survey methods would have been economically unviable. To make the most efficient use of scarce time and monetary resources we propose that the monitoring and tracking of biological invasions of a recognisable terrestrial animal species can be carried out through straightforward citizen surveys, given an amenable and appropriately distributed human population, as opposed to hair-tube field surveys. Close monitoring of an accumulation curve of survey responses could indicate to researchers or managers when the majority of the benefit, in terms of numbers of reports or unique locations, has been achieved in order that they may avoid unnecessary input of time and resources. Indeed, the stated objectives of this citizen science survey were largely fulfilled within the first 6-12 months of the programme though the time period of highest productivity will likely vary with each project. Hair-tube surveying is efficient and cost-effective when compared with live trapping methods for detecting mammal species presence (Garden *et al.* 2007) and is a valuable technique when employed to assess species presence in sites or habitats of specific interest. Fundamental volunteer sighting surveys, of the variety utilised in the current study, are more suited to acquiring the broad landscape level species presence information needed to conservatively locate and track an invasion front than targeted field surveys. Basic citizen science surveys can be attuned to the early detection of new arrivals to an area, because rare and different species are preferentially reported (Dickinson *et al.* 2010), but these techniques may be less appropriate when the species of interest is less charismatic or noticeable to the general public. In such cases survey organisers may find that more elaborate volunteer reporting protocols,

such as repeated records from defined transects or the requirement of certain survey methodologies (Gaidet-Drapier *et al.* 2006; Tulloch *et al.* 2013a), are necessary to acquire the desired detection data, which may in turn increase monetary and time expenditure.

Ideally decisions regarding management and exclusion of an alien species are formulated before its arrival (Leung *et al.* 2002) though a quick response to a recent arrival can improve outcome (Myers *et al.* 2000). Management response to an invading species should be informed by up-to-date knowledge of the current location of the species and movement trends. Basic citizen science projects can provide information on range expansion in a timely and cost-efficient manner, which should improve the efficiency and efficacy of management response to species invasions.

2.5 Thesis discussion

The foregoing manuscript has been accepted for publication in *Wildlife Research*. The following paragraphs provide additional detail on survey methodology and discussion.

2.5.1 Additional methods: citizen science survey

As declared, the website and survey were originally designed by Dr Emma Sheehy in 2009 as part of her PhD research into squirrel and pine marten distribution in the Irish midlands. Information regarding the current survey to locate the grey squirrel invasion frontier, which was originally known as the "Munster Squirrel Survey", was added to the survey website in November 2010 and survey responses to the questionnaire, already in use by Emma Sheehy, were requested from the public in the Munster region. In January 2012, data collection began for a national squirrel distribution survey using the same website form, and sighting reports were analysed on a county-by-county basis by the survey team. Responsibility for the region covered in the current chapter remained with the author at all times. The online survey form asked the following questions worded exactly as below:

1. Name:
2. Postal address:
3. Contact phone number:
4. Email address:
5. Name of forest/woodland/townland:
6. Name of closest town/village/post office:
7. Ordnance survey reference:
8. Woodland type (broadleaf, mixed, coniferous):
9. If squirrels seen, what species are they (red, grey, both)

10. When was the most recent sighting of red squirrels (within the last 3 months, 3 months to a year, over a year ago)?

11. When was the most recent sighting of grey squirrels (within the last 3 months, 3 months to a year, over a year ago)?

12. Type of squirrel sighting (personal observation, roadkill etc.):

13. Have pine martens been seen at this location (yes, no, don't know):

14. Type of pine marten sighting (personal observation, roadkill etc.):

15. Any other information you think may prove useful (e.g. surrounding land use, local grey squirrel control programs etc…):

The survey website is no longer available online as all of the projects using the site have completed data collection. Sighting reports were also received from volunteers by telephone and by post.

2.5.2 Additional discussion: room for survey design improvement

Questionnaires used for data collection should incorporate a pilot study during design for the purpose of identifying problematic questions or other issues (White *et al.* 2005). Due to budgetary and time constraints a pilot study was not used in the design of these survey questions. Changes to survey wording and layout were not appropriate given that the southern grey squirrel frontier survey project was utilising a pre-existing and active survey from a closely related project. The results in the manuscript above show that large quantities of scientifically valuable sighting reports were collected in Munster over the two-year survey period. With the benefit of hindsight, however, there was scope for some minor improvements in survey design.

The question on the website form above (8) suffered from some shortcomings: 1) no guidance was given on how to identify the three forest types, 2) the only choices were forest habitats, and 3) an answer was not required in this field for submission

and it was often left blank by respondents. Due to these design flaws, answers from this question were not analysed in the Munster region. Simple changes in question wording and answer layout may have led to the collection of valuable data on the frequency of the different types of habitat in which the public observe squirrels. Question phrasing such as "In what habitat type did the squirrel sighting take place?" would have improved volunteer comprehension. More answer choices that could be selected by radio buttons (the round selection spaces that only allow for one response) may have led to higher quality responses. Possible habitat responses should include at least the following types: broadleaf woodland, mixed woodland, conifer woodland, scrub, pasture, crop land, hedgerow, urban parkland, urban area, housing estate/suburban, industrial area, and other – with a blank to fill in. Each habitat choice must be accompanied by a short one-sentence description to allow for identification. As redesigned, this survey question would have provided analyzable data and insight into the types of habitat in which the public observe squirrels.

Members of the public often only responded with a townland name as a sighting location. Secondary follow-up contact, by phone or email, was frequently required in order to clarify the exact geographic location of the sighting. Location data collection could have been streamlined and made more accurate by using a map within the survey form in which respondent could "drop a pin" or read coordinates of the sighting location in addition to providing place names.

Though these improvements would have allowed for the streamlined collection of location and habitat data, their absence does not weaken the results of the survey in its current form. Great time and care were taken to ensure the accuracy of reporting locations and the problematic habitat data responses were not analysed.

Chapter 3 –

Personality traits are influenced by fixed states, labile states and individual differences in the grey squirrel

Counting breaths for the breathing rate personality test

Abstract

The relatively new field of animal personality or behavioural syndromes is yielding important insights into animal behavior. To date most of the focus has been on understanding whether and how consistent behavioural variation is adaptive but less attention has been given to exploring the extent to which the expression of personality traits might change with state. Furthermore, much of the research in the field has been conducted in captive populations but the significance of personality for animal behaviour under natural conditions remains largely unclear. Two introduced populations of the eastern grey squirrel (*Sciurus carolinensis*) were tested to understand whether personality is linked to fixed and labile states. All traits examined were significantly repeatable. The fixed states of sex, and the labile state of reproductive condition, influenced some of the measured personality traits – namely docility, and alarm vocalization. Female squirrels were more docile than males, and females who were reproductively active exhibited signs of greater stress when handled, compared to those who were inactive. The personality traits of docility, physiological stress response, and vocalization also differed between the two populations, although the magnitude and direction of the effects varied between traits. However, the observed state effects influenced both between individual and within individual variation equally, and thus did not cause individual differences. These data support the idea that the expression of personality traits is likely to be influenced by both additive genetic and state dependent variation.

3.1 Introduction

Personality can be defined as consistent behavioural differences between individuals, across time or context, involving single or multiple inter-correlated traits that form behavioural syndromes within populations (Sih *et al.* 2004a; Sih *et al.* 2004b; Ferrari *et al.* 2013). Behavioural ecologists have traditionally focused on single traits but the concept of personality or temperament emphasizes that individual differences in lone traits may reflect variation in a range of correlated functional behaviours. Thus the identification of personality within individuals emphasizes that behavioural plasticity may be constrained by these potentially complex correlations between and within traits. Most commonly, the approach has been to focus on traits, such as boldness, activity, aggression, reactivity, and sociality, which are easily measured under standardized experimental conditions, and to examine consistency across contexts, or to ask what their implications are for a range of functional behaviours, life history choices, or fitness. For example, exploration behavior is said to be an assay of the reactive-proactive behavioural phenotype axis and is known to predict a whole range of functional behaviours, such as interactions with conspecifics or competitors (Johnson and Sih 2007), willingness to take risks (van Oers *et al.* 2004b), sexual promiscuity (Réale *et al.* 2009; Scantlebury *et al.* 2010), and dispersal tendency (Bremner-Harrison *et al.* 2004; Rehage and Sih 2004).

To date much of the focus in the field has been to examine the hypothesis that personality variation reflects life history variation and is thus likely to be under selection (Dingemanse and Réale 2005; Réale *et al.* 2007; Quinn *et al.* 2009). Indeed a range of personality traits are reported to influence, or to have links with, fitness or life history strategies (Cote *et al.* 2008; Smith and Blumstein 2008; Dammhahn 2012). Similarly a number of studies have demonstrated that personality traits have an additive genetic basis (Dingemanse *et al.* 2004; van Oers *et al.* 2004a) and that some traits are genetically correlated (Duckworth and Kruuk 2009; Korsten *et al.* 2010), pointing to the evolutionary significance of personality. Although personality has been defined as consistent within the individual, regardless of

changing state (Réale *et al.* 2007), an increasing number of studies point to the importance of state, whether morphological, physiological or environmental, in the expression of personality types, though the relative importance of state and other intrinsic factors (for example, genetic or permanent environmental effects) in driving personality variation remains unclear.

The role that individual personality plays in determining life history alternatives such as dispersal tendency, response or susceptibility to parasitism, cohort, or fitness, such as survival and reproductive success, has been well probed in wild populations (Dingemanse and Réale 2005; Nussey *et al.* 2007; Réale *et al.* 2007). Theoretically, differences between the fixed or labile states of individuals within a population may help to maintain multiple personality types in the face of selection (Dingemanse and Wolf 2010; Wolf and Weissing 2010), though, in empirical studies, the potential effects of state on personality expression or vice versa have been largely overlooked. Exploration behaviour, for example, is a personality trait that several studies have shown is related to dispersal (Dingemanse *et al.* 2003; Cote *et al.* 2010a); although one study showed a genetic basis for this relationship (Korsten *et al.* 2010), another found that the difference between immigrants and residents in the same species was largely state (body size or the number of immigrant or resident parents for offspring) dependent (Quinn *et al.* 2011). A relationship between the speed of exploration and long term variability in faecal cortisol levels in the eastern chipmunk (*Tamias striatus*) was reported in a study that did not consider state effects such as breeding condition, body size, and weight (Montiglio *et al.* 2012). More recently, state (birth cohort, environment) was shown to have a relationship with this personality trait in the same species (Montiglio *et al.* 2014). In the case of parasite infection, personality may play a role in determining risk of exposure to infection or may be influenced by infection status. Dunn *et al.* (2011) found that a range of personality traits were mediated by two single states (parasite infection status and sex) as well as the interaction between them. More active/exploratory and bolder (male only) chipmunks (*Tamias sibiricus* and *T. striatus* respectively) were found to support higher loads of parasites (Boyer *et al.* 2010; Patterson and Schulte-Hostedde 2011) but, crucially, the state effects of

reproductive condition and body size, both of which have ecological importance, were not considered for *T. sibiricus* where both sexes were tested. With regard to fitness, two studies on *Tamiasciurus hudsonicus* demonstrated the influence of personality on overwinter female survival (Boon *et al.* 2008) and offspring fitness (Boon *et al.* 2007) but neither study considered the effects of states related to dominance and reproductive success in sciurids (body mass and size; (Wauters and Dhondt 1995; Wauters and Lens 1995)). Thus the complex interplay between state-driven personality expression or personality-driven state and fitness or life history requires more attention in behavioural studies of wild sciurid populations.

Given the observed potential for state variables to influence individual personality, there exists a need to elucidate the relationships between state and personality, in order to enhance the understanding of the correlation between personality traits and fitness. This is particularly true in species for which sex, breeding condition, age, and size are thought to be related to social dominance and reproductive success. Sciurid rodents are such species (Thompson 1978b; Gurnell 1987; Steele and Koprowski 2001), and as such are a good model for examining the influence of personality on inter- and intra-sexual competition for mates and food resources (Boon *et al.* 2007; Patterson and Schulte-Hostedde 2011). Many sciurids are polygynous, with both sexes capable of mating with multiple partners, during the breeding season and females providing sole parental care (Koprowski 1992). Multiple males may participate in scramble competition over access to females who are in oestrous for a single day. Male reproductive success is influenced by the ability to locate an oestrous female (Schwagmeyer and Woontner 1986), the ability to expand home range to encompass the ranges of many females (Kenward 1985; Wauters *et al.* 2000), competitive strategy (Wauters *et al.* 1990; Koprowski 1993), and dominance rank, although the relative importance of each factor likely varies between species (Dewsbury 1982). Female squirrels enter oestrus if they achieve a minimum body weight (Lurz *et al.* 2005), which is related to their dominance (Wauters and Dhondt 1989) and their ability to establish a home range in good habitat (Wauters and Dhondt 1995; Wauters and Lens 1995). Thus success in acquiring and exploiting good home ranges, and locating and winning mates may be

mediated or constrained by personality traits, which are commonly associated with these functional behaviours. Both bolder and more active/exploratory individuals in many species have shown greater proficiency at foraging and competing for resources (Dall *et al.* 2004; Ward *et al.* 2004; Lane *et al.* 2009), and may succeed more frequently in locating and chasing mates (Boon *et al.* 2008; Boyer *et al.* 2010; Patterson and Schulte-Hostedde 2011).

Dingemanse and Wolf (2010) suggest that if a personality trait shows state-dependency then variation in personality should be predicted by observed variation in state. This hypothesis was explored within the structure of the complex mating and social system of the eastern grey squirrel (*Sciurus carolinensis*), by quantifying the influence of static and changeable states (site, sex, reproductive condition, body size and body mass) on observed personality expression, and asking whether this drives individual differences. Though personality has been closely examined in other sciurid rodents during the last decade, the personality of the grey squirrel has not received much study (but see Pasitschniak-Arts and Bendell (1990)) though its ecology is well-documented (Koprowski 1994). Similar methods employed in previous sciurid personality studies were used as part of a live trapping programme to measure individual grey squirrel personality differences expressed during handling. It was hypothesized that it would be possible to identify repeatable personality traits in grey squirrels with these simple tests alone. The study was designed to test whether observed behavioural consistency could be explained by state differences present within grey squirrel populations or by a combination of state, and of consistent individual differences reflecting fitness driven variation. If a component of grey squirrel personality is state driven then, after controlling for other factors, a change in consistency should be observed as state changes. Otherwise, if evolutionary selection acts on personality variation in this species then an individual's personality should be observed to govern fitness (i.e. coming into a reproductively active condition).

3.2 Methods

3.2.1 Study area and species

Fieldwork was conducted in two forested sites in the Republic of Ireland managed by the Irish state forestry company, Coillte (Figure 3.1). Site 1, Cahir Park, (CP; 31.5 ha; 52° 21' N; 7° 55' W) is a mature deciduous woodland dominated by pedunculate oak (*Quercus robur*), European beech (*Fagus sylvatica*) and common ash (*Fraxinus excelsior*) but also containing elm (*Ulmus glabra*), sycamore (*Acer pseudoplatanus*), yew (*Taxus baccata*) and laurel (*Prunus laurocerasus*), and is managed as a public amenity. The majority of the forested area is arranged linearly (approximately 100 – 200 m in width) on the eastern bank of the River Suir south of Cahir town in Co. Tipperary with an additional 7 ha occurring as a block on the directly opposite western bank. Site 2, Kilnamack Wood, (KM; 247 ha; 52° 20' N; 7° 44' W) is located south of Clonmel town in Co. Waterford and is managed as commercial forest and for biodiversity. The trapping area was arranged in two contiguous blocks of mature forestry that were dominated by sessile oak (*Quercus petraea*), Scots pine (*Pinus sylvestris*), Douglas fir (*Pseudotsuga menziesii)* and sitka spruce (*Picea sitchensis*) with European beech, pedunculate oak, holly (*Ilex aquifolium*), rowan (*Sorbus aucuparia*) and yew also present.

Eastern grey squirrels are native to eastern North America (Koprowski 1994) but have been present in Ireland since 1911 when 12 individuals were introduced from populations already present in Great Britain (O'Teangana *et al.* 2000a). Grey squirrels are diurnal, mainly arboreal rodents who tolerate significant overlap in their home ranges (MacKinnon 1978; Don 1983), sometimes nest in groups (Koprowski 1996), and are active year round. Antagonistic behavior is most intense during the spring and autumn dispersal periods between resident and immigrating individuals (Thompson 1978b). At the start of the trapping programme, grey squirrels were known to have been present in CP for approximately 10 years and in KM for approximately 2 years (information received during citizen science survey,

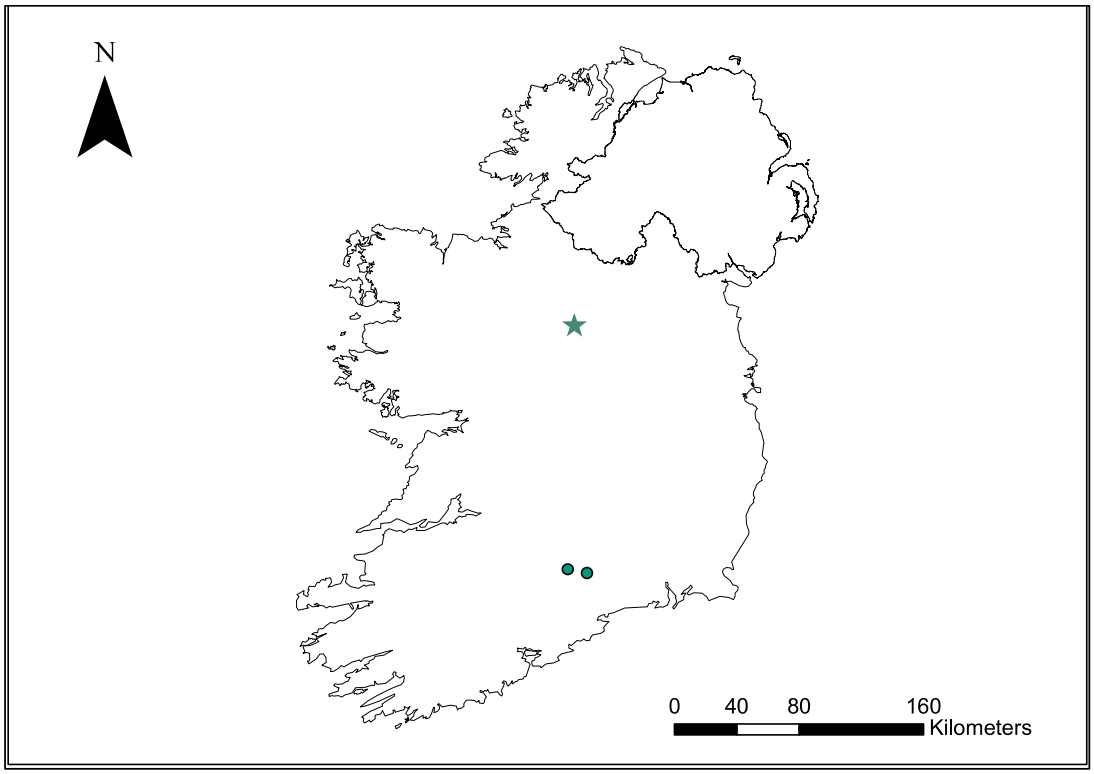


Figure 3.1 Green circles indicate the locations of *Sciurus carolinensis* trapping sites in Ireland; Cahir Park (CP) is west of Kilnamack Wood (KM). The original location of the 1911 grey squirrel introduction is indicated by the star.

chapter 2). These sites were both located near the expanding southern range frontier of the grey squirrel (chapter 2).

3.2.2 Trapping and Marking

The animals were captured on grids of 28 traps (single capture STV076 Defender small cage traps; STV International Ltd., Norfolk, UK), which were set out in each site to cover the total area of CP and a proportion (effective trapping area: 35.7 ha) of KM (Figure 3.2). The effective trapping area was calculated by extending the trapped area beyond the trapping grid by 100 m, the average radius of a grey squirrel home range, as in Kenward *et al*. (1998). The traps were modified with a wooden baseboard and nest box in order to reduce trapping stress. Trap placement and design similar to those utilised here have since been shown to effectively reduce trapping stress in squirrels (Bosson *et al.* 2012; Bosson *et al.* 2013). Squirrels were live-trapped in CP between 19 September 2011 and 30 May 2013 and in KM

between 20 November 2011 and 6 June 2013. Measurements related to the personality experiment were recorded from 19 March 2012 through to the end of the trapping program. Traps were placed in shaded cover at a density of approximately 1 trap/ha between 0 and 1.8 m from the ground in the branches of chosen trees and were baited with whole hazelnuts and a 4:1 mixture of whole maize and shelled peanuts (Lawton and Rochford 2007; Waters and Lawton 2011) so that both the trap and the yellow maize would be visible to squirrels from the canopy (Shorten 1954). Trapping sessions consisted of an eight-day sequence repeated every five weeks. Traps were pre-baited and locked open on days 1 and 3 and were set at dawn and checked between 4 and 6 hrs later on days 5 – 8. The eighth day of the session in the first site coincided with the first day of the session in the second site. Live trapping and tagging work was conducted under licences issued by the Irish National Parks and Wildlife Service.

All captured squirrels were marked with Trovan Unique ID-100 Passive Integrated Transponder (PIT) tags (MID FingerPrint Ltd, Dorset, UK) injected subcutaneously at the scruff during first capture (Poole and Lawton 2009). Captured squirrels were moved from the trap into a hessian sack for the handling test (see below) before being moved into a 250 x 70 mm metal mesh cylindrical handling cone for further observation. Once in the handling cone the squirrel was scanned with the LID571 PIT tag reader (Dorset Identification BV, Aalten, Netherlands) to establish identity. The breathing rate test (see below) was conducted prior to ascertaining the breeding condition and sex of the squirrel. Each squirrel was classified as displaying one of three breeding conditions, for each sex, at each capture (adapted from Wauters and Dhondt (1993)). The breeding conditions for females were 1) nipples absent (NA) indicating a non-breeding condition, 2) nipples visible (NV) where the nipples were easily visible but small, or 3) nipples swollen (NSW), where the female displayed signs of lactation, including baldness around enlarged nipples, indicating that such females had successfully produced a litter. Male breeding conditions were defined as 1) testes abdominal (TA) indicating a non-breeding condition, 2) testes semiscrotal (TSS) signifying sub-peak breeding condition, or 3) testes scrotal and large (TSL) for males in peak breeding condition, where the testes were fully

descended into the scrotum and were larger than 2 cm in length. Each squirrel was weighed to the nearest 10 g using a 1 kg Pesola spring balance and the right shin-bone length was measured to the nearest 0.1 mm using dial calipers to ascertain body size (Lawton and Rochford 2007; Poole and Lawton 2009).

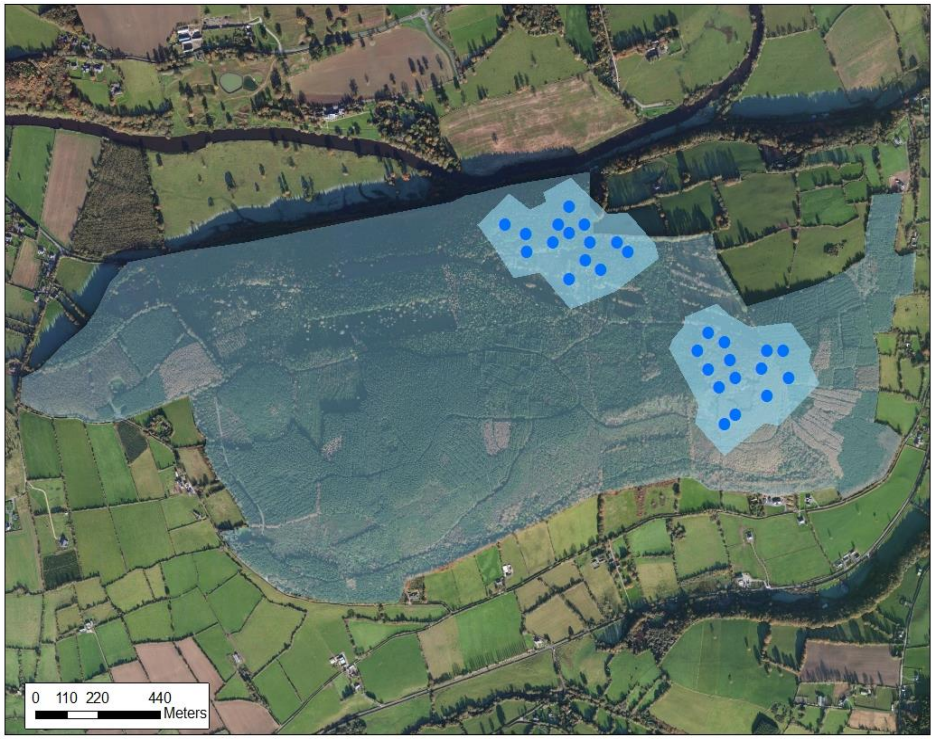
3.2.3 Behavioural Tests

To measure docility the squirrel was immediately moved from the trap into a 800 x 420 mm hessian cloth bag each time it was captured (Boon *et al.* 2007; Martin and Réale 2008; Patterson and Schulte-Hostedde 2011; Montiglio *et al.* 2012; Taylor *et al.* 2012). The handling bag was placed flat on the ground and the observer's knee held the bag shut while the number of seconds that the squirrel spent moving within the bag was counted for 30 seconds with a stopwatch (the struggle rate or SR). The stress response of the animal was measured by counting its breathing rate (breaths per 10 s; BR) using a stopwatch (Boon *et al.* 2007). Vocalization noises emitted by the squirrel were recorded between the observer's first approach to the trap and the release of the squirrel from the handling cone at the completion of measurement collection. Two distinct categories of vocalization were recorded: aggressive (AGG) and alarm (ALM). Aggressive vocalization consisted of growls and tooth chattering whereas screeches and barks or *kuks* were recorded as alarm vocalizations (Lishak 1982; Lishak 1984; Gurnell 1987; Pasitschniak-Arts and Bendell 1990; Steele and Koprowski 2001; Boon *et al.* 2008). The trapping history of each marked squirrel was recorded to obtain a measure of trappability, which has been linked to boldness in other species (Réale *et al.* 2000).

3.2.4 Statistical Analyses

All statistical analyses were carried out in SPSS 20.0.0 (Armonk, NY: IBM Corp.)

a) Cahir Park



b) Kilnamack Wood

Figure 3.2 On the previous page: locations of squirrel traps in a) Cahir Park and b) Kilnamack Wood with entire property (more transparent blue) and effective trapping area in Kilnamack Wood (less transparent blue).

3.2.4.1 Repeatability and Correlations

The repeatability of each measured behavioural trait among adult individuals over time was verified using the intra-class correlation coefficient calculated from the results of one-way ANOVAs, using the trait as the dependent variable and squirrel ID as the fixed effect (Lessells and Boag 1987). Excessive duplication in the repeatability calculation was removed by including only the first observation recorded from an individual in any one 4-day trapping session. The presence of behavioural syndromes, or suites of correlated behaviours, was examined in this system using the non-parametric Spearman's rank correlation coefficient ($p \leq 0.05$) to test for correlations between any of the four measures of behavioural responses, as well as body mass and body size (shin bone length).

3.2.4.2 Hypothesis tests

To test the hypothesis that state dependent effects drive personality in the grey squirrel a set of linear mixed models (LMM) was run in which the behavioural observations comprised the dependent variables. Prior to analysis behavioural observations made during the first capture of each squirrel in a trapping session were log-transformed. Specifically, a restricted maximum likelihood LMM (Nussey *et al.* 2007) was run on each of the four observed responses (SR, BR, AGG, and ALM), using date, year, study site, breeding status, capture number, leg length, and body mass as fixed effects. Squirrel identity was included as a random effect. No interactions were included in the model to prevent overparameterization. The inclusion of squirrel identity allowed the avoidance of pseudoreplication, caused by multiple observations of individuals and to estimate the variance in each trait due to the fixed effects (Boon *et al.* 2007). For comparison, a further set of LMMs was run that were identical to the first except for the inclusion of sex in place of breeding

status as a fixed effect. For the sake of simplicity, the results from the models that included sex are shown unless breeding status showed significance (Table 3.3). Significant values for fixed effects were considered conservatively, due to violations of the assumption of normality by all traits. The residuals of the LMM for all four behavioural traits differed significantly from the normal distribution ($p \leq 0.001$) and SR, AGG and ALM were noticeably zero inflated. The non-parametric Kruskal-Wallis test was used to further investigate significant effects, identified by the LMMs, on an aggregated subset of the data (mean observed value) extracted to remove the pseudoreplication of multiple observations per individual squirrel within the relevant fixed effect category. After confirmation of the significance of a fixed effect with the Kruskal-Wallis test, that effect was removed and the relevant LMM run again. The repeatability of the trait calculated from each version of the model (r^2 = subject variance/(subject variance + residual variance)) was compared with and without the significant fixed effect. A large difference in the repeatabilities would indicate that state had a large influence on individual behavioural consistency outside of personality. Where breeding status was significant, post-hoc pairwise comparisons of breeding statuses within each sex (again using LMMs), were used to determine which states showed significant differences.

The effects of the fixed states, sex and site, were examined for their influence on the trappability of a circumscribed group of 30 squirrels, which were captured between January and June in both 2012 and 2013, using a restricted maximum likelihood LMM. Squirrel identity was included as a random effect. The dependent variable was defined as the number of captures between January and June in the given year, while the fixed effects were sex, site, and the minimum number of days that each individual was known to be present in the site (date of last capture – first capture + 1) in each year. The repeatability of trappability was calculated using subject and residual variance as above.

3.3 Results

All adult personality traits were highly repeatable (Figure 3.3). Consistent individual differences were observed in the response to handling in all four of the measured traits. Summary statistics of the responses in the four behavioural tests are presented in Table 3.1. Responses in the struggle rate test varied from complete stillness to struggling for the entire 30 seconds of the test. A mean value of 27.94 ± 3.87 breaths per 10 s was observed in the captured squirrels though a considerable range was recorded. Squirrels tended to either vocal frequently or be non-vocal. Those that made either an aggressive or an alarm vocalization were likely to call repeatedly during handling and were significantly likely to produce the other type of vocalization. Some significant correlations were found between the behavioural measures themselves and between the measures and body mass and body size (Table 3.2). Breath rate was negatively correlated with both body mass and body size. Both types of vocalization were positively correlated with body size.

Personality trait model results are displayed in Table 3.3. Struggle rate was influenced by the sex ($p = 0.002$) of the squirrel and the site ($p = 0.049$) of capture (Figure 3.4a). Both breath rate ($p = 0.019$) and aggressive vocalization ($p < 0.001$) were significantly influenced only by site (Figure 3.4b). Breeding status, the only labile state considered, remained a significant influence on the alarm vocalization trait after the Kruskal-Wallis test was performed (Figure 3.5). Specifically, this significance was due to the difference between inactive (NA) and active (NV, $p = 0.015$; NSW, $p = 0.043$) reproductive states. Reaction norms of mean alarm vocalization for squirrels that were observed in more than one breeding status were plotted (Figure 3.6) to look for trends in behavioural plasticity linked to changing state. There were no clearly identifiable trends and a LMM, which included the squirrel*breeding status interaction as a random effect, did not find this term to be significant for this trait ($p = 0.745$), though sample size was small. Further models for each sex using the first capture of a squirrel in each reproductive state did not show that breeding status was influential (females: $p = 0.553$; males: $p = 0.351$) or that changing state resulted in squirrels altering their behaviour consistently. The

trappability of a squirrel was influenced only by the minimum number of days it was present in the trapping site and not by the state variables of site location or sex. The removal of significant fixed effects from personality trait models did not greatly alter the associated repeatability of the trait (Table 3.4).

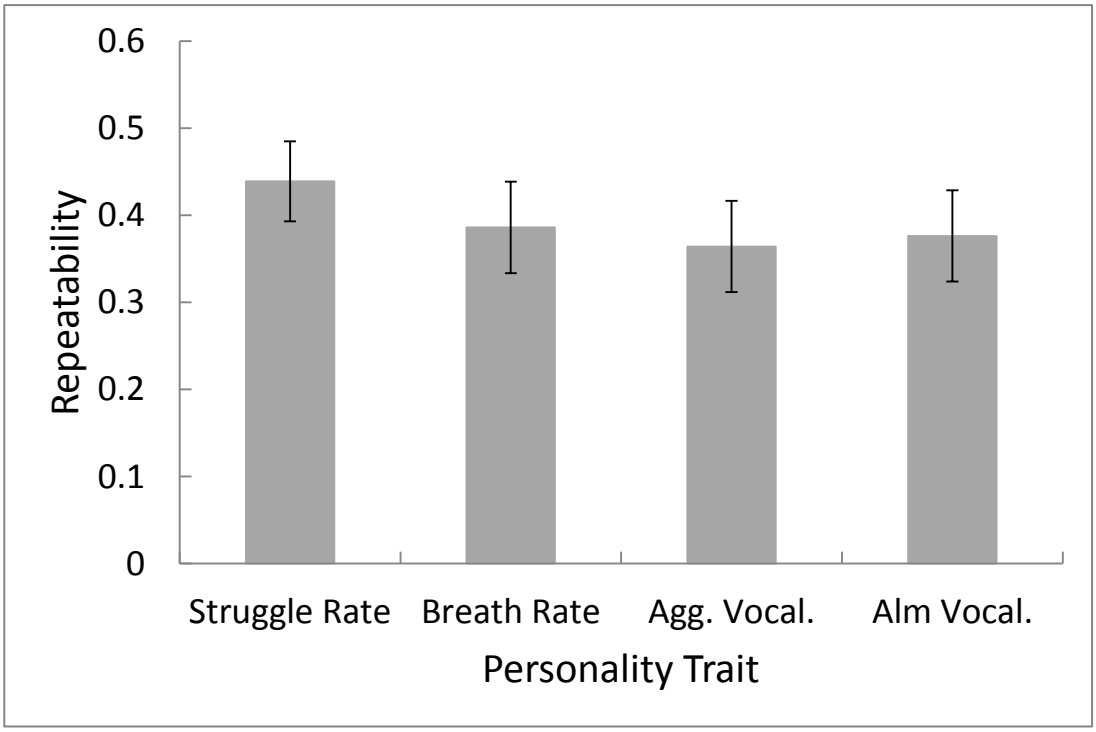


Figure 3.3 Repeatability of observed *Sciurus carolinensis* personality traits. The repeatability and standard error of each of the four observed personality traits (struggle rate, breath rate, aggressive vocalization and alarm vocalization) were calculated using the intraclass correlation coefficient. N (squirrels) = 101, N (observations) = 439.

Table 3.1 Summary statistics for the four behavioural tests used to assess *Sciurus carolinensis* personality at two sites in Ireland: struggle rate, breath rate, aggressive vocalization and alarm vocalization.

	Behavioural Trait Test					
	Struggle Rate					
	N	Min – Max	Mean ± SD	Median	Skewness	Kurtosis
All	439	0 – 30	17.37 ± 9.02	20	-0.656	-0.772
Males	253	0 – 30	18.49 ± 8.21	20	-0.787	-0.294
Females	186	0 – 30	15.84 ± 9.84	20	-0.436	-1.253
CP	348	0 – 30	17.57 ± 8.97	20	-0.658	-0.734
KM	91	0 – 30	16.62 ± 9.23	20	-0.653	-0.914
	Breath Rate					
All	437	14 – 39	27.94 ± 3.87	28	-0.265	0.249
Males	252	14 – 39	28.19 ± 3.82	28	-0.314	0.933
Females	185	18 – 37	27.61 ± 3.92	28	-0.196	-0.522
CP	347	14 – 39	27.60 ± 3.85	28	-0.306	0.303
KM	90	20 – 37	29.28 ± 3.66	29	-0.070	-0.253
	Aggressive Vocalization					
All	439	0 – 36	2.03 ± 5.02	0	3.606	14.907
Males	253	0 – 28	2.02 ± 4.74	0	3.212	10.901
Females	186	0 – 36	2.05 ± 5.39	0	3.956	18.039
CP	348	0 – 36	1.51 ± 4.56	0	4.501	23.358
KM	91	0 – 28	4.03 ± 6.11	1	2.095	4.583
	Alarm Vocalization					
All	439	0 – 30	1.11 ± 3.22	0	4.803	28.562
Males	253	0 – 20	0.89 ± 2.15	0	4.305	21.800
Females	186	0 – 30	1.41 ± 3.98	0	4.465	23.270
CP	348	0 – 23	0.80 ± 2.49	0	2.494	30.359
KM	91	0 – 30	2.26 ± 4.98	0	3.419	13.679

Table 3.2 Non parametric Spearman's rank correlation of the body mass, size, the four observed personality traits and trappability in two populations of eastern grey squirrels, *Sciurus carolinensis*, in Ireland.

Correlations between personality traits and trappability are for 30 squirrels, which were captured between January and June in 2012 and 2013. Significant correlations are indicated with asterisks (* if $p < 0.05$, ** if $p < 0.01$, *** if $p < 0.001$).

	Body Mass	Body Size	Struggle Rate	Breath Rate	Agg. Voc.	Alm Voc.	Trap.
Body Mass	-	0.387***	0.032	-0.103*	0.027	0.006	-
Body Size	0.387***	-	-0.041	-0.165**	0.128**	0.119*	-
Struggle Rate	0.032	-0.041	-	0.03	0.09	0.046	0.067
Breath Rate	-0.103*	-0.165**	0.03	-	0.131**	0.012	0.058
Agg. Voc.	0.027	0.128**	0.09	0.131**	-	0.228***	0.172
Alm Voc.	0.006	0.119*	0.046	0.012	0.228***	-	0.107
Trap.	-	-	0.067	0.058	0.172	0.107	-

Table 3.3 Coefficient, F-test, and P value for the intercept and each fixed effect in the linear mixed models that explored the relationship between state and five personality traits (struggle rate, breath rate, aggressive vocalization, alarm vocalization, and trappability) in two populations of eastern grey squirrels, *Sciurus carolinensis*, in Ireland.

The fixed effect of sex is shown here for models where breeding status was not significant for the sake of simplicity. The random effects in these models are shown in Table 3.4.

	Behavioural Trait Test		
	Struggle Rate		
	Coefficient	*F* test	P
Intercept	4.060±1.623	$F_{1,413}$=6.610	**0.010**
Sex*	-0.514±0.158	$F_{1,98}$=10.606	**0.002**†
Body mass	0.001±0.001	$F_{1,429}$=1.764	0.185
Body size	-0.028±0.021	$F_{1,426}$=1.693	0.194
Site‡	0.383±0.192	$F_{1,101}$=3.988	**0.049**†
Date	-0.001±0.001	$F_{1,425}$=2.887	0.090
Year§	0.227±0.164	$F_{1,319}$=1.922	0.167
Capture	0.002±0.010	$F_{1,296}$=0.051	0.821
	Breath Rate		
Intercept	3.842±0.248	$F_{1,387}$=239.358	<**0.001**
Sex*	-0.016±0.023	$F_{1,86}$=0.490	0.486
Body mass	0.000±0.000	$F_{1,429}$=0.070	0.792
Body size	-0.006±0.003	$F_{1,412}$=2.898	0.089
Site‡	-0.066±0.028	$F_{1,90}$=5.697	**0.019**†
Date	0.000±0.000	$F_{1,422}$=1.062	0.303
Year§	-0.057±0.025	$F_{1,296}$=5.255	**0.023**
Capture	-0.001±0.001	$F_{1,258}$=0.588	0.444
	Aggressive Vocalization		
Intercept	0.324±1.403	$F_{1,417}$=0.003	0.957
Sex*	0.025±0.139	$F_{1,104}$=0.033	0.857
Body mass	0.000±0.001	$F_{1,428}$=0.181	0.671
Body size	0.009±0.018	$F_{1,428}$=0.260	0.610
Site‡	-0.612±0.168	$F_{1,107}$=13.225	<**0.001**†
Date	0.001±0.001	$F_{1,425}$=2.117	0.146
Year§	-0.211±0.142	$F_{1,327}$=2.199	0.139
Capture	0.014±0.008	$F_{1,308}$=2.779	0.097

Table 3.3 cont. Coefficient, F-test, and P value for the intercept and each fixed effect in the linear mixed models that explored the relationship between state and five personality traits (struggle rate, breath rate, aggressive vocalization, alarm vocalization, and trappability) in two populations of eastern grey squirrels, *Sciurus carolinensis*, in Ireland.

The fixed effect of sex is shown here for models where breeding status was not significant for the sake of simplicity. The random effects in these models are shown in Table 3.4.

		Behavioural Trait Test		
		Alarm Vocalization		
		Coefficient	*F* test	P
Intercept		-0.911±1.226	$F_{1,251}$=0.525	0.469
Breeding Status**	NA	0.055±0.123	$F_{5,258}$=2.695	0.658
	NV	0.303±0.150	$F_{5,258}$=2.695	**0.046**†
	NSW	0.325±0.131	$F_{5,258}$=2.695	**0.015**†
	TA	-0.130±0.105	$F_{5,258}$=2.695	0.217
	TSL	0.108±0.105	$F_{5,258}$=2.695	0.302
Body mass		-0.001±0.001	$F_{1,418}$=4.153	**0.042**
Body size		0.031±0.016	$F_{1,306}$=3.564	0.060
Site‡		-0.290±0.119	$F_{1,49}$=6.002	**0.018**
Date		-0.001±0.000	$F_{1,416}$=1.079	0.299
Year§		0.140±0.121	$F_{1,230}$=1.336	0.249
Capture		-0.004±0.007	$F_{1,137}$=0.288	0.592
			Trappability	
Intercept		2.200±1.194	$F_{1,53}$=8.832	0.098
Sex*		0.356±1.018	$F_{1,26}$=0.123	0.729
Site‡		-0.950±1.033	$F_{1,27}$=0.846	0.366
Min. days present		0.316±0.067	$F_{1,41}$=21.961	<**0.001**

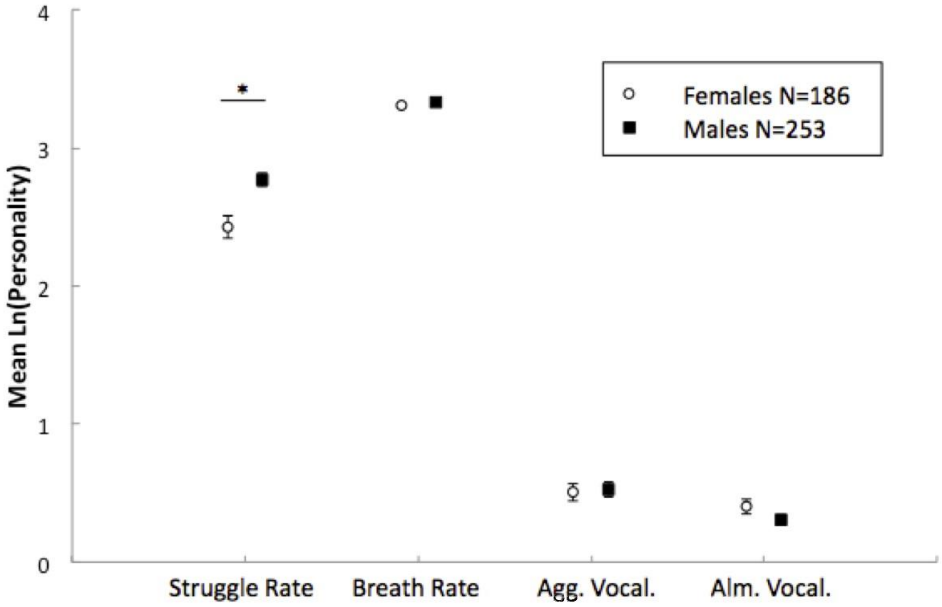
*Male was considered for the reference for sex in the model.
†Also significant in Kruskal-Wallis test.
‡Site KM was considered the reference for site in the model.
§Year 2 (2013) was considered the reference for year in the model.
**TSS was considered the reference for Breeding Status in the model.

Table 3.4 Repeatabilities (r^2) and subject and residual variances of the linear mixed models that tested relationship between state and five personality traits (struggle rate, breath rate, aggressive vocalization, alarm vocalization, and trappability) in two populations of eastern grey squirrels, *Sciurus carolinensis*, in Ireland.

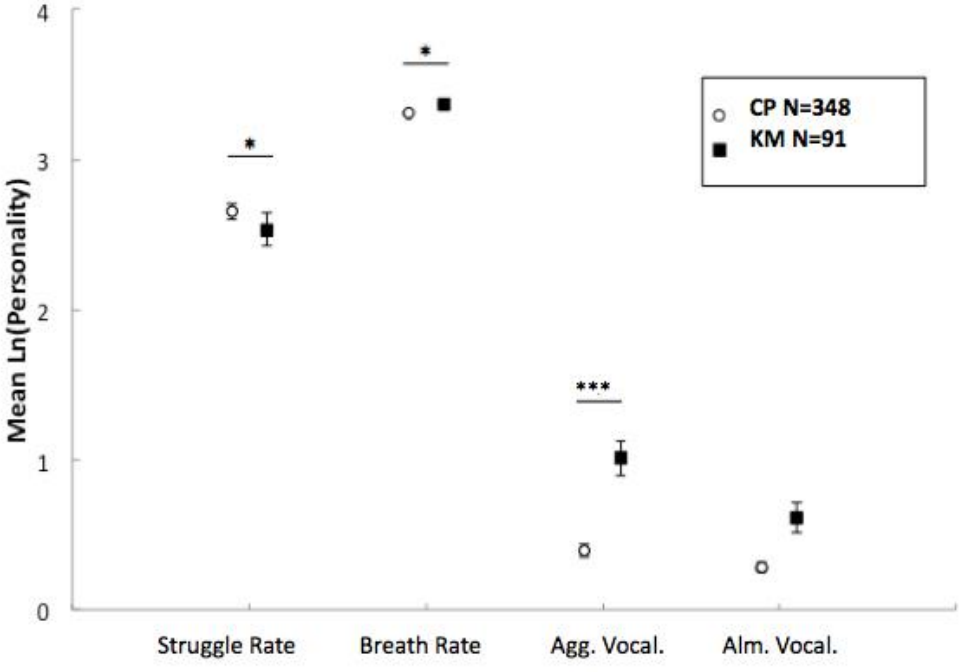
The fixed effects of these models are reported in Table 3.3. The influence of significant fixed effects on the repeatability of the personality trait was examined by running restricted models for the trait with the effect removed.

			Subject			Residual		
Trait	Model*	r^2	Variance	Wald Z	P	Variance	Wald Z	P
Struggle Rate	Full	0.400	0.367±0.077	4.798	<0.001	0.548±0.042	13.191	<0.001
	Sex	0.431	0.416±0.084	4.940	<0.001	0.549±0.042	13.152	<0.001
	Site	0.402	0.370±0.078	4.759	<0.001	0.551±0.042	13.153	<0.001
	Sex + Site	0.427	0.411±0.084	4.901	<0.001	0.551±0.042	13.129	<0.001
Breath Rate	Full	0.333	0.007±0.002	4.146	<0.001	0.014±0.001	13.044	<0.001
	Site	0.333	0.007±0.002	4.385	<0.001	0.014±0.001	13.070	<0.001
Agg. Voc.	Full	0.423	0.289±0.058	5.029	<0.001	0.404±0.030	13.263	<0.001
	Site	0.456	0.340±0.065	5.184	<0.001	0.406±0.031	13.208	<0.001
Alm Voc.	Full	0.196	0.093±0.040	2.307	0.021	0.378±0.031	12.101	<0.001
	BRST	0.240	0.129±0.045	2.656	0.008	0.374±0.031	12.145	<0.001
Trap.	Full	0.217	2.343±2.211	1.060	0.289	8.477±2.272	3.732	<0.001

*Designation in this column indicates which significant effect was removed from the full model



3.4a



3.4b

Figure 3.4 Mean values with standard error of grey squirrel (*Sciurus carolinensis*) personality traits for a) male (filled square) and female squirrels (open circle), and b) squirrels in Cahir Park (Site 1, open circle) and Kilnamack Wood (Site 2, filled square). Values have been log transformed and asterisks indicate a significant difference (* if $p < 0.05$, ** if $p < 0.01$, *** if $p < 0.001$).

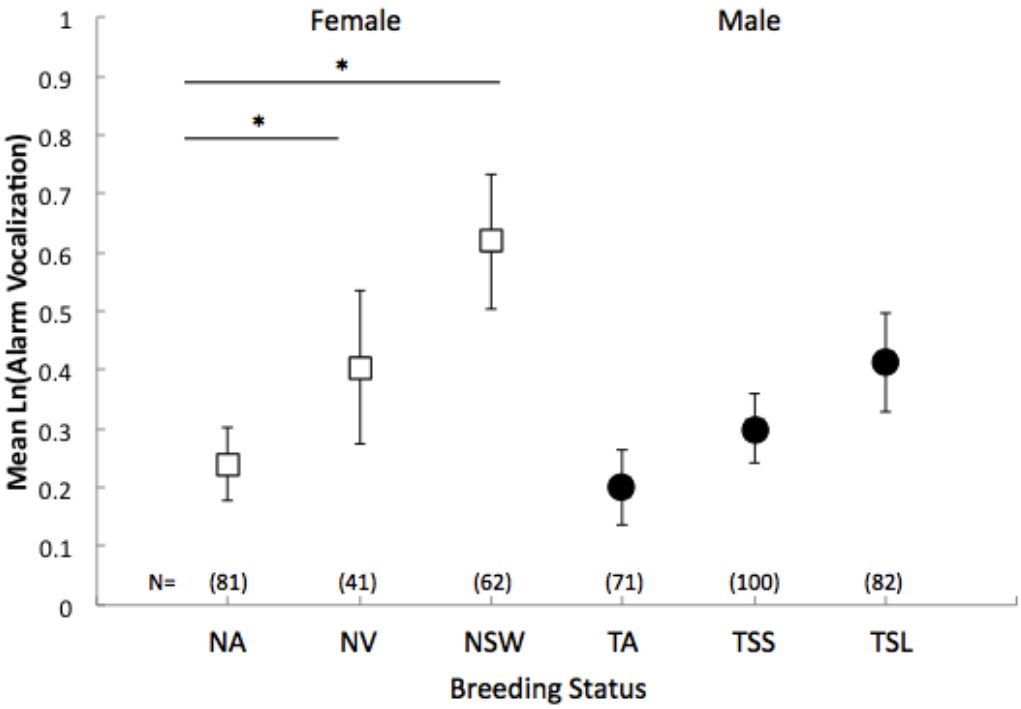
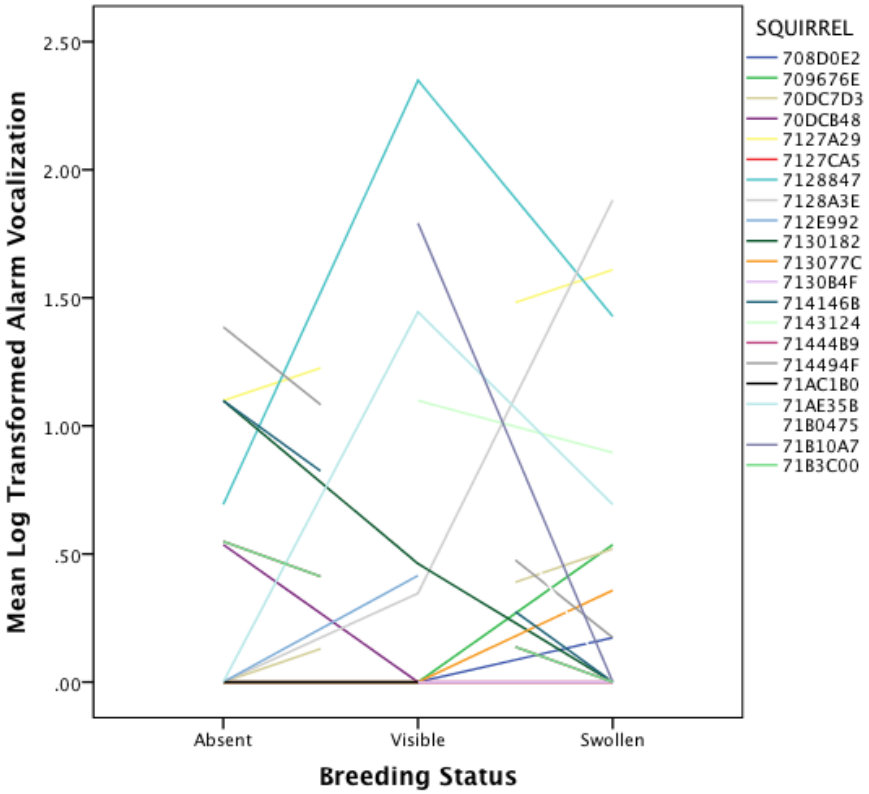
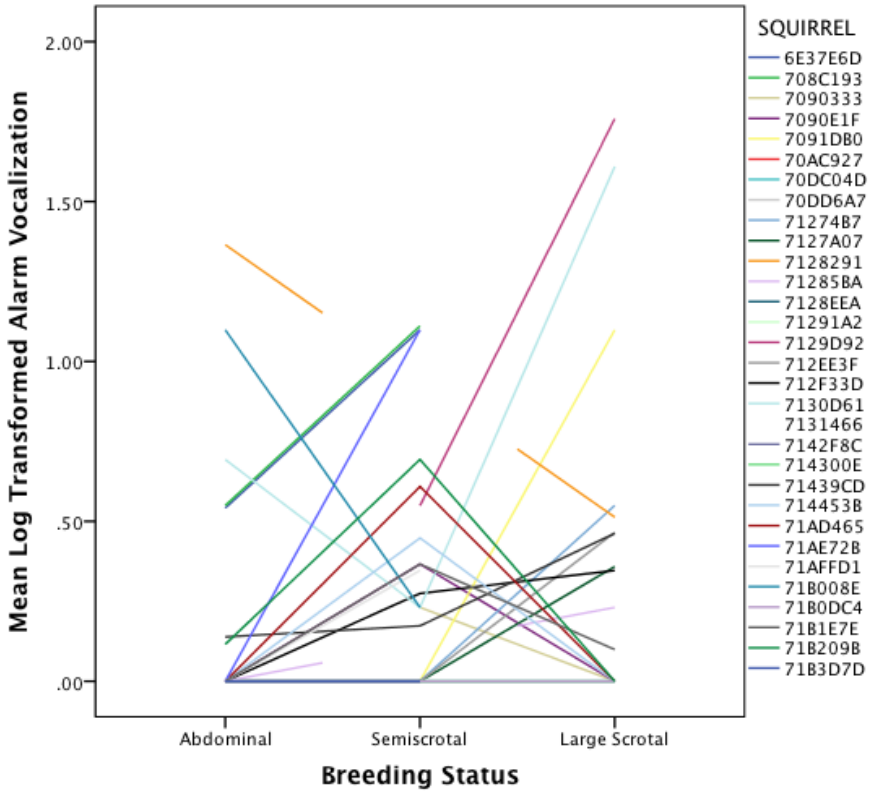


Figure 3.5 Mean values with standard error of the alarm vocalization personality trait for grey squirrels (*Sciurus carolinensis*) in each reproductive state (nipples absent (NA), nipples visible (NV), and nipples swollen (NSW) for females and testes abdominal (TA), testes scrotal (TSS), and testes scrotal and large (TSL) for males). Active reproductive statuses are NV and NSW for females, TSS and TSL for males – see text for a thorough explanation of each reproductive status. Values have been log transformed. Actively reproductive females (NSW, $p = 0.043$; NV, $p = 0.015$) were significantly different in this trait than non-active females.


Mean Log Transformed Alarm Vocalization
2.50
2.00
1.50
1.00
.50
.00
Absent
Visible
Swollen
Breeding Status
SQUIRREL
708D0E2
709676E
70DC7D3
70DCB48
7127A29
7127CA5
7128847
7128A3E
712E992
7130182
713077C
7130B4F
714146B
7143124
71444B9
714494F
71AC1B0
71AE35B
71B0475
71B10A7
71B3C00

3.6a


Mean Log Transformed Alarm Vocalization
2.00
1.50
1.00
.50
.00
Abdominal
Semiscrotal
Large Scrotal
Breeding Status
SQUIRREL
6E37E6D
708C193
7090333
7090E1F
7091DB0
70AC927
70DC04D
70DD6A7
71274B7
7127A07
7128291
71285BA
7128EEA
71291A2
7129D92
712EE3F
712F33D
7130D61
7131466
7142F8C
714300E
71439CD
714453B
71AD465
71AE72B
71AFFD1
71B008E
71B0DC4
71B1E7E
71B209B
71B3D7D

3.6b

Figure 3.6 On the previous page: reaction norms of a) female squirrels with nipples absent, visible and swollen and b) males with testes abdominal, semiscrotal, and large scrotal for mean log transformed alarm vocalization. This personality trait was the only trait that was examined that showed a significant effect of the labile breeding condition state. Only squirrels that were observed in more than one reproductive state are shown.

3.4 Discussion

In the analyses it was possible to identify significantly repeatable personality traits in two populations of introduced eastern grey squirrels through observation of behaviours exhibited due to handling stress. The evidence suggests that these personality traits are partially influenced by fixed and labile states. The site in which a squirrel lived influenced the physiological stress response and level of aggression displayed to humans when handled. The sex of a squirrel partially explained its docility. Among the labile states considered in this system, only breeding status significantly influenced the expression of personality traits with reproductively active females emitting alarm calls more often than squirrels in other reproductive states. Neither body mass nor body size was found to significantly influence any of the personality traits we considered. Therefore, although social position may be influenced by weight and size (Gurnell 1987) this does not appear to extend to personality in this species.

3.4.1 Repeatability and correlations of personality traits

Docility, or time spent active in the handling bag, is repeatable and has been linked with struggle rate in sciurids and other mammals (Réale *et al.* 2000; Martin and Réale 2008; Montiglio *et al.* 2012; Taylor *et al.* 2012; Ferrari *et al.* 2013). Individuals showing a consistently higher struggle rate are considered to be less docile in their response to humans. Tonic immobility, the converse of struggle rate, has also been shown to be repeatable in domesticated pigs and birds (Erhard *et al.* 1999; Groothuis and Carere 2005). However, reports of correlations between personality and struggling behaviour are inconsistent in the literature. Associations

between struggle rate and bold and active-exploratory personalities were observed in some studies of North American red squirrels and eastern chipmunks (Boon *et al.* 2007; Montiglio *et al.* 2012), but no correlation between these traits was recorded in others (Martin and Réale 2008; Patterson and Schulte-Hostedde 2011). Struggle rate in grey squirrels showed no correlation with the responses of other measured personality traits or body mass or body size.

Few studies have examined breath rate in a behavioural context and there is a paucity of information on how measures of breath rate may relate to repeatable personality traits in animals. Cardiac parameters, similar to respiration rate, are controlled by the autonomic nervous system and have been used as indicators of emotionality and stress response (Koolhaas *et al.* 1997). Ferrari *et al*. (2013) found significant between-individual repeatability in wild ground squirrel breathing rates, as did Boon *et al*. (2007) in a wild population of tree squirrels. Higher breath rates have been noted in shyer individuals (Carere and van Oers 2004) and were also correlated with active and aggressive temperaments (Boon *et al.* 2007). In the current study, both body mass and body size were significantly negatively correlated with breath rate, though this negative correlation may be due to the well known negative scaling of physiological processes that occurs in animals as body size increases (Lindstedt and Calder III 1981) and perhaps unrelated to personality.

Propensity to vocalize, or number of vocalizations, has rarely been considered in the context of personality research. Vocalization repeatability has not, to date, been examined in wild populations, although in domesticated piglets the number of vocalizations was not repeatable (Ruis *et al.* 2000). In an aggression test the number of grunts made by North American red squirrels was recorded but did not figure in subsequent principal component analysis (Boon *et al.* 2007; Boon *et al.* 2008). In pairwise grey squirrel aggression tests, vocalizations corresponding to the "alarm" type in the current study were seen as indicators of submission while "aggressive" type vocalizations were interpreted as threatening behaviour though repeatability was not determined (Pasitschniak-Arts and Bendell 1990). The current study has shown, for the first time in a wild mammal, that the vocalization trait is significantly

repeatable and that alarm and aggressive vocalizations are correlated. Stressed grey squirrels, with high breath rates, were significantly more likely to vocalize aggressively. A significant positive correlation was also observed between an individual's size and tendency to vocalize, which corresponds to previous work in piglets that found body mass and vocalization similarly correlated (Erhard *et al.* 1999). Struggle attempts also correlate with vocalization in piglets (Erhard *et al.* 1999; Ruis *et al.* 2000) though this was not observed to be the case in these grey squirrels.

Repeatable measures of trappability are associated with bold, risk-taking or active-exploratory personalities in birds (Mills and Faure 2000; Garamszegi *et al.* 2009) and mammals (Réale *et al.* 2000; Boon *et al.* 2008; Boyer *et al.* 2010; Patterson and Schulte-Hostedde 2011). Bold or active individuals are expected to take the risk of entering a trap for a food reward more often than shy or reactive individuals. Trappability was not found to be significantly repeatable in wild populations of grey squirrels and no correlations between trappability and other personality traits were found in this study. The restricted sample size of 30 individuals for which trappability scores were determined may well have hampered the ability of the study to find statistical significance and correlations between this and other traits as this was a smaller sample than other studies have used (Boon *et al.* 2008; Patterson and Schulte-Hostedde 2011).

3.4.2 Fixed effects of state on personality

Initially, it was predicted that reproductively active male squirrels would be less docile and would exhibit more aggressive personality than males in a non-reproductively active condition or females. The expression of such traits should contribute positively to the male squirrels' abilities to increase home range size, locate receptive females, and succeed in scramble competition for access to mating opportunities (Patterson and Schulte-Hostedde 2011). No difference was found in levels of aggression between the sexes or between male squirrels in active or non-

active reproductive states in any of the personality traits that were considered. The method of measuring aggression in the current study may explain this. Others studies measured aggression in sciurids with pairwise or mirror image stimulation tests (Pasitschniak-Arts and Bendell 1990; Boon *et al.* 2007; Boon *et al.* 2008) and these approaches may arguably be better at provoking an intraspecific aggressive response than stress induced through handling. Greater male reproductive success is associated with bolder and aggressive personalities in other species (Ariyomo and Watt 2012; Betini and Norris 2012). Female mate choice has been postulated to drive selection for bold and aggressive traits in males if they are an honest indicator of quality, fitness, or provisioning capabilities (Wolf *et al.* 2007; Schuett *et al.* 2010). Future studies, with the capacity to determine paternity in squirrels via genetic methods, would have more potential to observe the influence of male personality on reproductive success.

Female squirrels were recorded as actively reproductive after breeding only, when pregnancy, parturition, and lactation caused observable changes to the nipples. Originally, it was hypothesized that reproductively active females would be more aggressive and less docile and exhibit an increased tendency to alarm call than females that had failed to reproduce. Expression of these personalities should enhance the ability of reproductive females to defend and warn their young against predators and conspecifics. As with male squirrels, variation in female reproductive condition was unable to explain variation in docility or aggression. In the alarm calling trait, however, the fixed effect of breeding status controlled for a substantial proportion of the observed repeatability. Female squirrels in active reproductive states (NV and NSW reproductive statuses) alarm called significantly more frequently on average when handled compared to non-reproductively active female squirrels. Some of the repeatability of this trait was caused by within-reproductive status rather than within-individual consistency, underlining the importance of state in both the expression of personality and contributing to individual differences. This was shown in grey squirrels through inconsistency in the direction and size of the change in alarm calling behaviour as squirrels were observed in different reproductive states (Figure 3.6). That breeding status was not found to be a

significant effect when only the first capture in each status for a squirrel was included in the model, which further supports repeatability being controlled by within-status rather that within individual consistency. Altruism has been postulated to explain why reproductive adult female in ground squirrels (*Spermophilus beldingi*) alarm called more frequently than expected in the presence of kin (Sherman 1977; Shields 1980). Although it was not possible to identify or record familial relationships and weaning success in this study, the higher frequency of alarm calling in reproductively active females suggests the existence of nepotistic behaviour in grey squirrels.

Variation in personality has been linked to time since site colonization in studies performed along expanding species invasion frontiers, with aggressive individuals found more often at the leading edge (Duckworth and Badyaev 2007). In Ireland, the population of invasive grey squirrels is continuing to expand along the southern range frontier. Though both study sites are close to the invasion frontier (chapter 2), grey squirrels have been present in the locations for different lengths of time (10 years in CP; 2 years in KM). As expected, given previous research in edge population personality, squirrels in the more recently colonized site had higher breath rates and vocalized aggressively significantly more often than animals in CP. However, contrary to these expectations, squirrels in KM were also more docile in the handling bag than in CP. The differences in squirrel personality may also have been influenced by habitat quality differences between the two sites. Active individuals are able to acquire more food in rich habitats but are less effective at exploiting scarce resources (Tessier *et al.* 2000; Groothuis and Carere 2005; Boon *et al.* 2007). Martin and Réale (2008) found that chipmunks with burrows closer to public trails were more active than those with less exposure to human activity, a finding that helps to explain why grey squirrels were less docile and more active in the handling bag in the site with more human disturbance. Further work with more replication and control sites in established populations and the capacity to separate habitat, human disturbance, and time since colonization effects, would allow for stronger conclusions to be drawn on this question. In life history theory, site should influence behavioural decisions taken by an animal, in order to improve fitness and

therefore can be considered as a fixed state (Wolf and Weissing 2010). Results here highlight the importance of site effects on animal personality expression.

This initial investigation of grey squirrel personality found that both state and individual effects contribute to observed variation in personality. It was possible to identify repeatable personality traits in the responses of individuals to stress caused by human handling. Studies conducted in two wild populations of grey squirrels showed that variation in personality could be partially explained by variation in both labile and fixed states, including breeding status, sex, and site. The recorded significance of the breeding status state effect indicates that in this species personality influences or is influenced by reproductive fitness or life-history variation, though current methods did not allow for us to determine the direction of causation or parental weaning success. Future studies should seek to clarify the direction of influence between personality and breeding success in grey squirrels and how personality variation is associated with environmental or range expansion effects.

Chapter 4 –

Characteristics of frontier population dynamics of an invasive squirrel species: do introduced populations function differently than those in the native range?

On the left, a female squirrel that has given birth. On the right, a male squirrel in peak breeding condition

A manuscript based on this chapter is under review in an international peer-reviewed journal

Abstract

Several squirrel species are biological invaders and their establishment in an area is often marked by ecological and economic damage to native species and forestry crops. The eastern grey squirrel (*Sciurus carolinensis*) has been intentionally introduced multiple times outside of its native range but its success in establishing and spreading has not been consistent. An intensive live-trapping programme was designed to investigate the demography and population dynamics of invasion frontier populations of this species in the Republic of Ireland, a region marked by the slow but steady invasion of the grey squirrel. Low densities and high breeding rates distinguished these frontier populations. These results were placed in context with other frontier and established grey squirrel populations throughout the introduced and native range of this species. As expected, variation in invasion speed and severity of impact between regions were reflected in population demography. The highest densities, survival rates and breeding rates were recorded in Britain where the grey squirrel invasion has been most damaging. Careful comparative demographic study of invading populations could improve management outcomes, indicate differential invasibility of invaded communities, and offer clues to enhance the design of conservation reintroduction projects.

4.1 Introduction

A principal cause of worldwide biodiversity loss, after habitat destruction, is the anthropogenic introduction of species outside of their native range (Vitousek *et al.* 1997). Introduced species may impact the invaded ecosystem by modifying nutrient cycles, altering food web relationships, carrying diseases, or through competition with native species (e.g. Human and Gordon (1996); Kelly and Hawes (2005); Fukami *et al.* (2006); Sainsbury *et al.* (2008)). When invasive species advance through exclusion barriers and control measures are unsuccessful, longer term monitoring and management of expanding non-native populations becomes necessary (Bertolino and Genovesi 2003; Courchamp *et al.* 2003; Simberloff 2003). Detrimental effects of invaders are often realized after a lag phase, at which point the invader has become firmly established and attained problematic density levels (Mack *et al.* 2000). Though the most prominent ecological damage may occur in areas where invaders are established, an equally critical area for control and management is the expanding invasion frontier (Russell *et al.* 2009). The frontier of the invasion may be patchy, unpredictable in movement, and move at speeds and directions influenced by habitat connectivity and corridors or human-mediated transportation (Brown *et al.* 2006; Florance *et al.* 2011; White *et al.* 2012). An improved understanding of the population dynamics and demographics of invasive species range frontiers could clarify why invasive populations can exhibit divergent invasion success in different regions or ecosystems. As alterations in native species ranges become more common due to climate change (Parmesan 2006), the study of invasive frontier populations offers an opportunity to probe the underlying mechanisms of species range adaptation and movement (Elton 1958; Urban *et al.* 2008).

Recent invasion ecology research has focused on identifying and quantifying traits or characteristics common among successful invaders, so that management strategies and predictions of future impact might be better informed (Kolar and Lodge 2001). Introduced species that tend to become established or invasive often experience frequent introduction events (high propagule pressure), a match between

origin and destination habitat or climate, and a history of invasiveness (Kolar and Lodge 2001; Hayes and Barry 2008). More detailed characteristics common to invaders, such as life-history strategies or dispersal mechanisms, may be taxon or species-specific (Sakai *et al.* 2001; Hayes and Barry 2008). Recent work has postulated the existence of an "invasion syndrome" (Sih *et al.* 2004b) made up of traits common to successful invaders such as exploration, boldness and intra- and interspecific aggression (Rehage and Sih 2004; Chapple *et al.* 2012). Rodents, species of which are often either accidentally or purposefully introduced, possess many characteristics of successful invaders, and diverse rodent species have caused ecosystem-damaging effects in both island and continental regions (Simberloff 2009). Introductions and translocations of squirrel species are often purposeful, resulting from deliberate releases or, less commonly, from escapes from the pet or collections trade (Bertolino 2009). Deliberate introduction enhances the tendency of squirrel species to become invasive over accidentally translocated species, which must survive undetected on the transportation vector. Once released into the recipient habitat, squirrels tend to perform well as invaders as they possess non-selective diets (Bertolino 2009; Bertolino and Lurz 2013), an ability to thrive in both urban or more natural habitats (Jessen *et al.* 2010), the capacity to establish from a low number of founders (Wood *et al.* 2007), and an often favourable public perception which hampers control efforts (Bertolino and Genovesi 2003; Benitez *et al.* 2013).

The eastern grey squirrel, the most oft-introduced tree squirrel species (Bertolino 2009), is native to the eastern portion of North America (Koprowski 1994) but has been introduced to the European, African, and Australian continents as well as outside of its native range in North America (Bertolino 2009; Bertolino and Lurz 2013). Introduced grey squirrels were eradicated in Australia and have remained confined to afforested or urban environments in South Africa away from native ecosystems (Long 2003). Population expansion and negative ecosystem effects, however, have characterized the grey squirrel introduction events in Ireland, the United Kingdom, Italy, and western areas of North America. In these regions grey squirrels have been implicated in the decline of native squirrel species and damage

to forestry crops (Kenward and Parish 1986; Kenward and Holm 1993; Bruemmer *et al.* 2000; O'Teangana *et al.* 2000a; Wauters *et al.* 2000; Gonzales 2005; Sainsbury *et al.* 2008; Bertolino *et al.* 2014).

Grey squirrels are diurnal, mainly arboreal, rodents that tolerate significant conspecific home range (MacKinnon 1978; Don 1983) overlap and are active year round. Tree seeds predominate in the grey squirrel diet (Korschgen 1981) and annual variability in food resource availability has been linked to fluctuations in population density (Nixon *et al.* 1975; Gurnell 1983; Gorman and Roland 1989). Grey squirrels are polygamous (Koprowski 1992); and males, under scramble competition, vie for reproductive access to a female on the single day she enters oestrus during a breeding season (Koprowski 1993). There are two reproductive seasons in a year (Shorten 1954; Dubock 1979) and female breeding success in each season is determined by body condition, resource availability and home range quality. Dispersal is most common among the juvenile age class and occurs during the autumn and spring months (Thompson 1978a).

Exploration of population mechanisms at work in successful species invasions is beneficial both for the management and further study of invasive species, as well as population biology as a discipline, where these systems provide cases to examine basic range expansion and frontier dynamics as well as establishment processes (Sakai *et al.* 2001). To date, there has not been a comprehensive examination of population dynamics across the native and introduced ranges of the grey squirrel, a problematic mammalian invader. Ecosystem invasions by this species have not proceeded uniformly across all affected regions; with disparities noted, for example, in expansion rate (Okubo *et al.* 1989; O'Teangana *et al.* 2000a) and disease transmission (Gurnell *et al.* 2006) potentially pointing to variation in ecosystem invasibility. Previous studies have recorded grey squirrel dynamics in the native range as well as frontier and established populations in parts of Europe and North America. Here an examination of frontier grey squirrel populations in Ireland fills a critical knowledge gap by providing demographic information through intensive live-trapping. It is now possible, for the first time, to compare the demography and

dynamics of established and frontier grey squirrel populations across European introduction areas and established populations in the introduced and native ranges in North America. The results are placed in context with other established and frontier populations throughout the introduced and native range of the species to explore how variation in these factors could relate to invasion speed, invasibility, and severity of ecological consequences. Differences in scale, scope, and ecological consequences of grey squirrel invasions in different regions should be reflected in the demography and dynamics of established and frontier grey squirrel populations across the native and introduced range.

4.2 Methods

4.2.1 Live trapping demographic study

A live trapping study of frontier grey squirrel populations was carried out in two forested sites in the Republic of Ireland managed by the Irish state forestry company, Coillte (Figure 4.1). Cahir Park (CP; 52° 21' N; 7° 55' W) is a 31.5 hectare (ha) mature deciduous site dominated by pedunculate oak (*Quercus robur*), European beech (*Fagus sylvatica*) and common ash (*Fraxinus excelsior*) but also containing elm (*Ulmus glabra*), sycamore (*Acer pseudoplatanus*), yew (*Taxus baccata*) and laurel (*Prunus laurocerasus*). It is managed as a public amenity site and contains walking trails, minor roads, and parking areas. The majority of the forested area is arranged linearly (approximately 100 – 200 m in width) on the eastern bank of the River Suir south of Cahir town in Co. Tipperary with an additional 7 ha occurring as a block on the directly opposite western bank. Kilnamack Wood (KM; 52° 20' N; 7° 44' W) is a 247 ha property managed for commercial forestry and biodiversity objectives located south of Clonmel town in Co Waterford. The trapping area was arranged in two contiguous blocks of mature forestry that were dominated by sessile oak (*Q. petraea*), Scots pine (*Pinus sylvestris*), Douglas fir (*Pseudotsuga menziesii)* and Sitka spruce (*Picea sitchensis*) with European beech, pedunculate oak, holly (*Ilex aquifolium*), rowan (*Sorbus aucuparia*) and yew also present. Grey squirrels were known to be present in CP for

approximately 10 years and in KM for approximately 2 years (from responses to the citizen science survey, chapter 2) at the start of the live trapping programme.

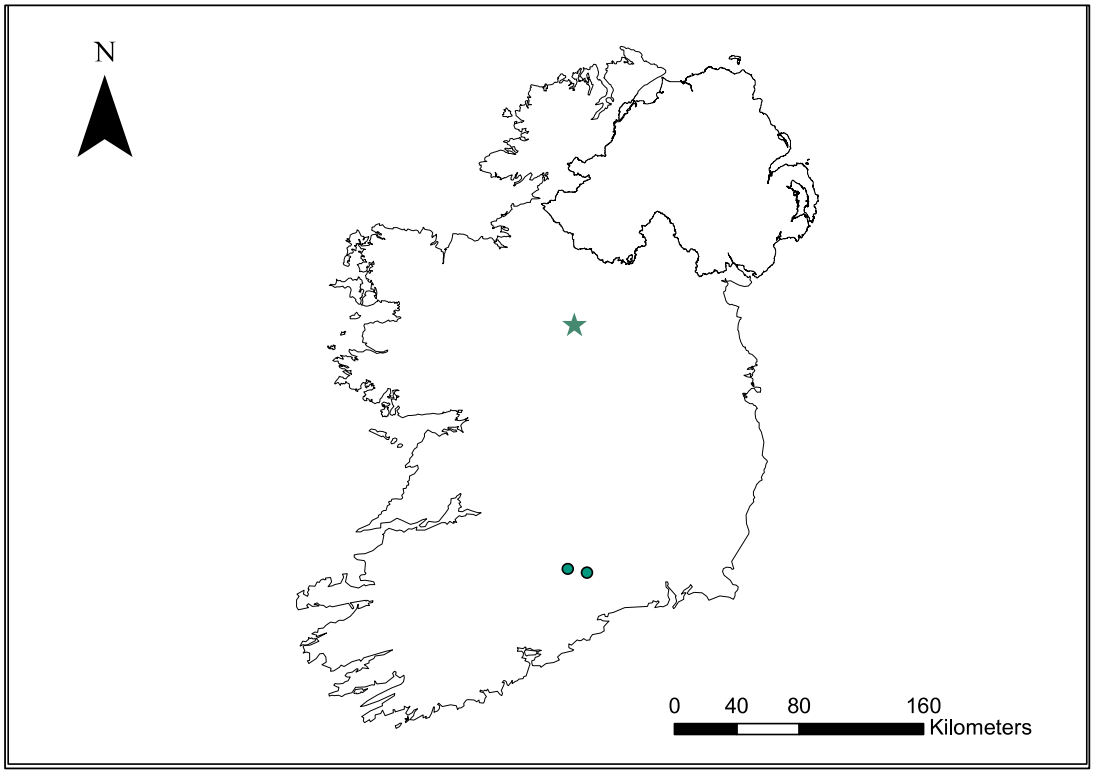
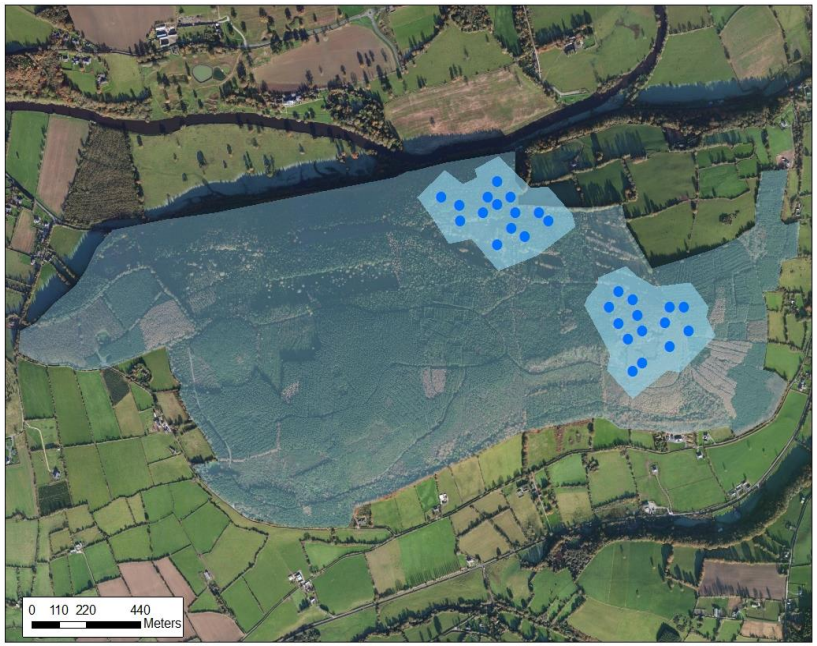


Figure 4.1 Locations of trapping sites in Ireland, Cahir Park is west of Kilnamack Wood. The original location of the grey squirrel introduction is indicated by the star.

Live squirrel traps (n=28 in each site) were set out in each site in a grid formation, covering the entirety of the 31.5 ha in CP and an effective trapping area of 35.7 ha in KM, where the trapping grid did not fill the woodland (Figure 4.2). The effective trapping area was calculated by extending the trapped area beyond the trapping grid by 100 m, the average radius of a grey squirrel home range, as in Kenward *et al*. (1998). Squirrels were trapped in CP between 19 September 2011 and 30 May 2013 and in KM between 20 November 2011 and 6 June 2013. Trapping sessions (n=18 in CP; n=16 in KM) consisted of an eight-day sequence repeated every five weeks. The animals were captured with single capture STV076 Defenders small cage traps (STV International Ltd., Norfolk, UK) modified with a wooden nest box and base board in order to reduce trapping stress. Traps were placed in shaded cover at a density of approximately 1 trap ha^{-1} between 0 and 1.8 m from the ground in the

a) Cahir Park



b) Kilnamack Wood

Figure 4.2 On the previous page: locations of squirrel traps in a) Cahir Park and b) Kilnamack Wood with entire property (more transparent blue) and effective trapping area in Kilnamack Wood (less transparent blue).

branches of a tree and were baited with whole hazelnuts and a 4:1 mixture of whole maize and shelled peanuts (Lawton and Rochford 2007; Waters and Lawton 2011). Although trap construction and placement in the current study was based on techniques utilised in Ireland and Britain over the last 30 years of squirrel research, Bosson *et al*. (2012; 2013) more recently showed that these techniques were effective in reducing the stress associated with live trapping. Traps were pre-baited and locked open on days 1 and 3 and were set at dawn and checked between 4 and 6 hrs later on days 5 – 8 inclusive. Live trapping and tagging procedures were conducted under licences issued by the Irish National Parks and Wildlife Service.

All captured squirrels were marked with Trovan Unique ID-100 Passive Integrated Transponder (PIT) tags (MID FingerPrint Ltd, Dorset, UK) injected subcutaneously at the scruff during the first capture event (Poole and Lawton 2009). Captured squirrels were restrained in a 250 x 70 mm metal mesh cylindrical handling cone while demographic and physical data were recorded. After the identity of each squirrel was established by scanning with a LID571 PIT tag reader (Dorset Identification BV, Aalten, Netherlands) the breeding condition and sex of the squirrel were recorded. Each squirrel was classed as displaying one of three breeding conditions for each sex at each capture (adapted from Wauters and Dhondt (1993)). The breeding conditions for females were nipples absent (NA), nipples visible (NV; where the nipples were easily visible but small), or nipples swollen (NSW; where the female displayed signs of current or recent lactation including baldness around enlarged nipples). NSW females were assumed to have successfully produced a litter. Male breeding conditions were defined as testes abdominal (TA), testes semiscrotal (TSS; testes palpable but < 2 cm in length), or testes scrotal and large (TSL; where the testes were fully descended into the scrotum and were larger than 2 cm in length). Males classed as TSL were in peak breeding condition. Each squirrel was weighed to the nearest 10 g using a 1 kg Pesola spring balance and the

right shin-bone length was measured to the nearest 0.1 mm using dial calipers as a measure of body size (Lawton and Rochford 2007; Poole and Lawton 2009).

4.2.2 Food resource availability

Tree seeds comprise the bulk of the grey squirrel diet during the summer and autumn seasons (Gurnell 1983) and the availability of this food resource contributes to over-winter survival and spring breeding success (Havera and Smith 1979; Wauters *et al.* 2008). Since the deciduous species present in the study area shed their seed by early December (Shaw 1968; Nielsen 1977; Gurnell 1993), tree seed availability was measured in January 2012 and 2013 in each site, after all seeds were assumed to have fallen from the canopy, to estimate the quality of the habitat and year. All tree seeds within 1 m^2 quadrats, placed in the sites at a density of 1 quadrat per 4 ha of deciduous or mixed tree species cover, were collected from the same locations each year and counted in the laboratory (n=7 in CP; n=4 in KM). The seed density of each tree species was calculated as the product of the mean number of seeds $quadrat^{-1}$ and the proportion of the site occupied by that species. Based on the calculated seed densities, the tree seed resource availability each year was classified as either good or poor in each site. Good resource availability for squirrels was defined as $\geq$ 30 beechnuts m^{-2} and/or $\geq$ 10 acorns m^{-2}; when densities did not reach these values the resources that year were recorded as poor (Wauters and Lens 1995).

4.2.3 Statistical methods

4.2.3.1 Physical data

A condition index was created to separate the effects of body size from body condition using a linear regression of log mean body mass on mean shin length using data from all adult grey squirrels from both study sites (log body mass = 0.022(±0.003)×(leg length) + 4.676(±0.233), R^2= 0.316, P<0.001, n=112). The condition index score for each adult squirrel consisted of the body mass residuals of

this regression model (Wauters *et al.* 2000). The significance of sex and site categories to mean body mass, leg length and condition index were examined with two-way ANOVAs (Wauters *et al.* 2000).

4.2.3.2 Reproduction and recruitment

Adult and subadult squirrels were separated based on body mass and breeding condition. Squirrels of each sex were classified as adult if they attained the minimum mass at which active breeding conditions were ever observed in each site (adult female: ≥ 510 g (CP), ≥ 570 g (KM); adult male: ≥ 440 g (CP), ≥ 460 g (KM), see also Ferryman *et al.*, (2006)). The spring breeding season occurred during March-June and the summer breeding season during August-November, based on observed female breeding condition in both sites. Female squirrels were assumed to have reproduced in a breeding season if they displayed the NSW breeding condition during that season. The breeding rate for each season and for the year 2012 was calculated by dividing the number of reproductive females by the total number of females present during that period. When calculating the overall 2012 breeding rate, females were counted as breeding regardless of whether they reproduced once or twice. After six months of trapping in each site all trappable resident squirrels were assumed to have been marked (to allow for acclimatization to traps) and thereafter all newly captured adults and subadults were defined as newly recruited (if captured ≥ 2 trapping sessions) or dispersing (if captured in only one trapping session). It was also possible to trace new subadults to their birth season (Kenward *et al.* 1998).

4.2.3.3 Density and survival estimation

The minimum number alive (MNA) method for estimating the number of individuals present in a trapping area has often been utilized to report squirrel population sizes or densities (Fischer and Holler 1991; Gurnell 1996; Wauters *et al.* 2000; Gurnell *et al.* 2004b; Wauters *et al.* 2004; Lawton and Rochford 2007; Verbeylen *et al.* 2009). The MNA method provides a conservative estimate of the

number of individuals present, which is comprised of all individuals recorded during a trapping session as well as those recorded previously and subsequently but not during the session. Due to high trapping success and the low number of unmarked squirrels caught after the acclimatization period it is likely that MNA estimates accurately reflect the trappable populations in these study sites. The densities of squirrels in each site during each season were examined using MNA estimates.

Estimates of recapture and survival probabilities were calculated using Program MARK (White and Burnham 1999). This program uses Cormack-Jolly-Seber (CJS) models to analyse the effects of sex, site, and time on survival (ϕ) and recapture (p) probabilities. Time was incorporated into the models in several ways (Wauters *et al.* 2008) either as "time" (all occasions separately), "quarter" (autumn, winter, spring, summer), "season" (summer, winter), "quarter-year" or "season-year" (where the quarter or season were separated by year). Capture data from each trapping session were combined into one sampling occasion and included data from the final 15 trapping sessions in each site in the model to lessen the impact of the acclimatization period at the beginning of the trapping programme.

The most saturated model including all parameters was defined as $[\phi_{sex*site*time}, p_{sex*site*time}]$ where ϕ represented the 5-weekly survival probability and p represented the 5-weekly recapture probability. The parametric bootstrap procedure was used to test the goodness-of-fit of the saturated model to ensure that the model adequately fit the data and did not violate the CJS assumptions. To quantify the overdispersion or extra binomial noise resulting from lack of fit or violation of assumptions the variance inflation factor ($\hat{c}$) was calculated from the quotient of the observed model deviance and the mean deviance of the simulated models. The value of $\hat{c}$ will be close to 1 if the assumptions are met, but $1 < \hat{c} < 3$ can be corrected for by inflating the variances of parameter estimates to reflect the overdispersion of the data set.

The candidate set of models was created by systematically stepping down the parameters on p, while retaining the most saturated survival function $[\phi_{sex*site*time}]$. Next, ϕ was stepped-down using the most parsimonious recapture function

(Lebreton *et al.* 1992; Wauters *et al.* 2008; Doherty *et al.* 2012). The Akaike Information Criterion corrected for small sample bias (AIC_c, or the quasi-AIC_c after the ĉ correction was made) identified the most parsimonious model that adequately represented the data. If $\Delta QAIC_c < 2$ then the models have approximately equal weight in the data. A $2 < \Delta QAIC_c < 7$ shows that there is considerable support for a real difference in the adequacy of the models while $\Delta QAIC_c > 7$ show strong support for such a difference (Anderson and Burnham 1999a; Anderson and Burnham 1999b).

Annual (50-week) survival and recapture probabilities were calculated from the product of the 5-weekly parameter estimates based on the selected model. The calculation of the standard error of the annual survival probability required the use of the delta method (or method of propagation of errors), because the sampling variance of the new parameter was a function of the sampling variances of the former parameters (Powell 2007). The method is based on a first-order Taylor series transformation, though the application of general rules can aid in calculating sampling variances (Powell 2007). It was not possible to use the same method to calculate the standard error of the recapture probability due to the complexity of the term in the model.

4.2.4 Comparative demography of grey squirrels

An extensive search of published literature, including unpublished PhD theses based in Ireland, on grey squirrel demography was carried out to aid in the identification of trends and differences in demographic parameters between native, as well as established and frontier introduced grey squirrel populations. All studies returned from the Google Scholar search "squirrel demograph*" which also included the phrase "*Sciurus carolinensis*" as well as relevant papers cited by the studies returned in the search were considered. To be included in the analysis the following conditions were required to be met:

1. Published in an international peer-reviewed format *or* a completed Irish PhD thesis.
2. Habitat clearly defined at least to the level of coniferous/mixed/deciduous.
3. Study area clearly defined and reported in ha or acres.
4. If the population was outside the native range the status of established or frontier must be discernible.
5. Method of data collection reported.
6. If data for a parameter were not reported in the format desired then they must be able to be simply calculated (e.g. calculating the mean body mass or annual survival rate from the monthly rate etc.)

Demographic data from studies that reported one or more of the following parameters for grey squirrels: population density, annual survival rate, breeding rate, litter size, juvenile recruitment, home range size, and body mass were compared. Formal statistical analyses, such as a meta-analysis, of these demographic parameters could not be performed due to missing values and a lack of standardization between the size and scope of the included studies. Values reported from studies of populations with the same region and habitat profile were averaged.

4.3 Results

4.3.1 Frontier trapping study

Grey squirrels were captured 1072 times in live traps during 3880 trap days. In total, 130 individual grey squirrels were trapped (CP: n = 99; KM: n = 31) with (re)capture number for each squirrel ranging from 1 to 38. The majority of captured squirrels were adults (n = 112). The first two sessions in CP and the first four sessions in KM were distinguished by low capture numbers and were considered to be the period during which the squirrels were becoming acclimatized to the traps. Excluding the acclimatization periods, a consistently higher mean density of grey squirrels was observed in CP (1.14 squirrels ha^{-1}) than in KM (0.38 squirrels ha^{-1}). The highest seasonal densities observed occurred during the 2012 spring season (April – June) in both sites (Figure 4.3).

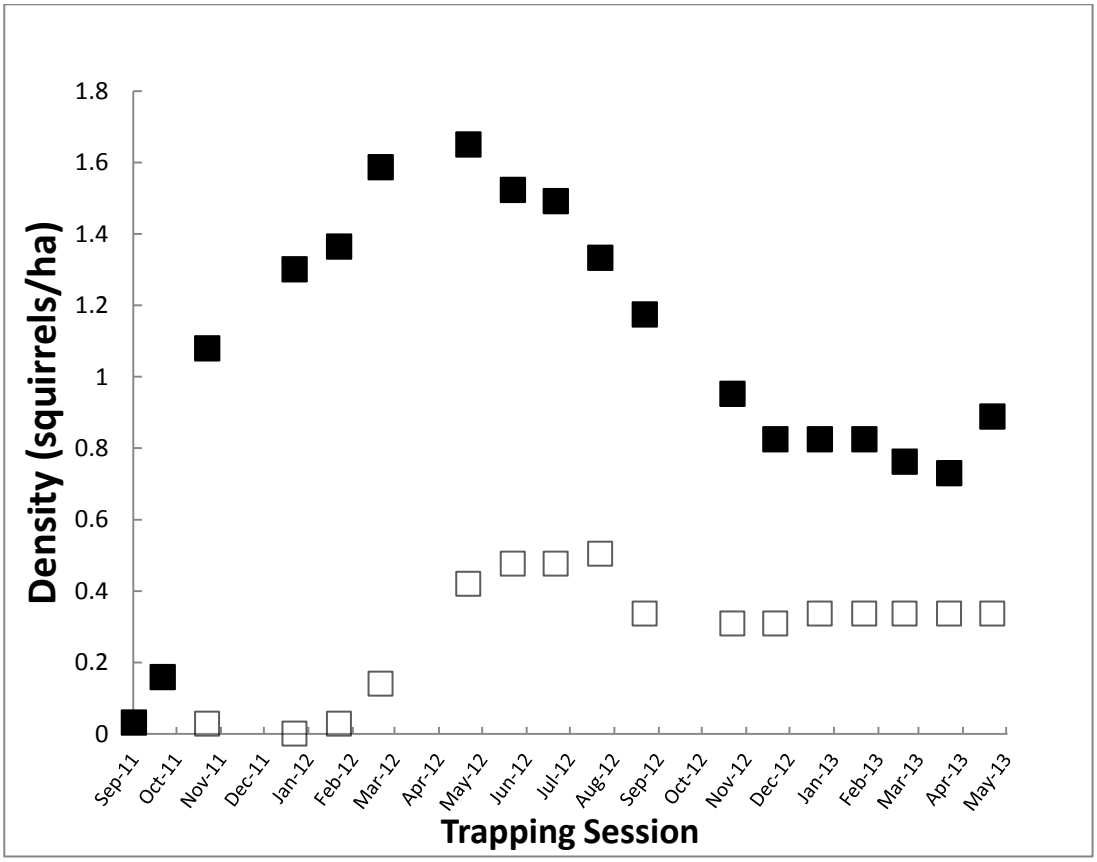


Figure 4.3 Density of grey squirrel (*Sciurus carolinensis*) calculated from minimum number alive population estimates generated during live trapping of two frontier populations (■: Cahir Park, □: Kilnamack) in the Republic of Ireland.

4.3.1.1 Habitat quality

The autumn 2011 tree seed crop was of good resource quality in both sites when collected in January 2012. The mean number of tree seeds m^{-2} for the dominant seed producing species in the sites, oak and European beech, is reported in Figure 4.4. In 2012 beechnuts and acorns exceeded the good resource level threshold in CP whereas in KM only beechnuts reached that level. The resource levels of the autumn 2012 crop were poor in both sites when collected in January 2013.

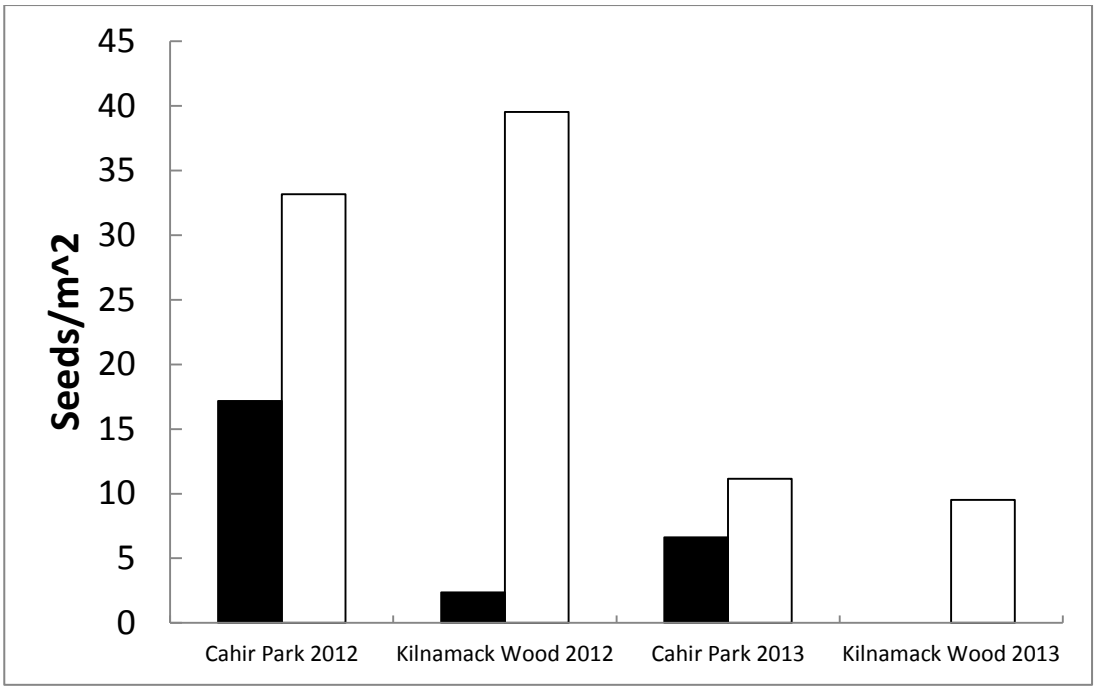


Figure 4.4 Mean number of tree seeds collected m^{-2} under tree cover, proportional to species coverage in the site, in Cahir Park and Kilnamack Wood live trapping study sites in the Republic of Ireland. Seeds collected in January comprised the seed crop of the previous autumn of ■ oak and □ European beech. Good resource years reached the threshold of ≥ 30 beechnuts m^{-2} or ≥ 10 acorns m^{-2}.

4.3.1.2 Physical characteristics, reproduction, and recruitment

The results of three separate two-way ANOVA models investigating the influence of the fixed effects of site, sex, and the interaction of site×sex on the dependent variables of body mass, body size, and body condition are shown in Table 4.1. The mean body mass of adult grey squirrels of both sexes was significantly greater in KM than in CP. Additionally, female squirrels in both sites weighed significantly more than males, though a site×sex interaction in mean body mass was not recorded. There was no observed sexual dimorphism in body size, as measured by shin-bone length, though squirrels in KM were significantly larger than those in CP. No site×sex interaction was observed for body size. The site effect disappeared when the dependent variable of body condition was investigated though females in both sites were in better condition than male squirrels. These results suggest that though the grey squirrels in KM were heavier than their counterparts in CP, this was in

proportion to a larger mean body size and squirrels in KM were not in better body condition.

Table 4.1 The results of three two-way ANOVAs for adult grey squirrel (*Sciurus* carolinensis) body mass, leg length, and condition index score from two sites in Ireland.

The fixed effects of site, sex and their interaction were included in all three models. Significant results are in bold.

Dependent Variable	Fixed Effect	n	Mean (±SD)	df	F	p
Body mass	Site	21 (KM); 91 (CP)	580±48 g (KM); 565±48 g (CP)	1,108	5.697	**0.019**
	Sex	47 (F); 65 (M)	585±44 g (F); 555±46 g (M)	1,108	12.826	**0.001**
	Sex*Site			1,108	1.542	0.217
Body size	Site	21 (KM); 91 (CP)	77.3±1.7 mm (KM); 76.1±2.3 mm (CP)	1,108	5.256	**0.024**
	Sex	47 (F); 65 (M)	76.6±2.1 mm (F); 76.1±2.3 mm (M)	1,108	1.202	0.275
	Sex*Site			1,108	0.001	0.975
Condition	Site	21 (KM); 91 (CP)	-0.004±0.998 (KM); 0.001±1.001 (CP)	1,108	1.329	0.252
	Sex	47 (F); 65 (M)	0.355±0.004 (F); -0.256±0.999 (M)	1,108	11.399	**0.001**
	Sex*Site			1,108	1.912	0.170

The sex ratio in both frontier populations was slightly male biased (Table 4.2). The majority of adult females produced litters during both the spring and summer breeding seasons in both sites in 2012 (overall 2012 breeding rate: 67.9% CP; 75% KM). However, very few females successfully reproduced during the spring breeding season in 2013. Although subadults were traceable to the breeding season of their birth, high numbers of squirrels in this age group were not captured. There were no captures of subadults during the spring of 2013 that would have originated from the summer 2012 breeding season. New adult squirrels captured between May 2012 and June 2013 were designated as recruits or dispersers, according to the number of trapping sessions during which they were captured. Squirrels, adult or subadult, that were caught for the first time during the final trapping session in 2013

were not included in the analysis presented in Table 4.2 because their recruitment status could not be determined.

Table 4.2 Demographic and reproductive data collected from two frontier populations of grey squirrels (*Sciurus carolinensis*) during a 22-month live trapping programme in the Republic of Ireland.

The number of litters, breeding rate, and litters per reproducing female were calculated using the number of females exhibiting signs of recent or current lactation in either the spring (March-June) and/or summer (August-November) breeding season. New subadults could be traced to the breeding season of their birth.

		Cahir Park Sep 2011 - May 2013			Kilnamack Wood Nov 2011 - June 2013		
		female	male	total	female	male	total
N		45	54	99	13	18	31
Sex ratio (%M)			54.55			58.06	
Litters	spr 2012		13			3	
	sum 2012		15			1	
	spr 2013		2			0	
Breeding rate	spr 2012		52%			100%	
	sum 2012		60%			50%	
	spr 2013		15%			0%	
Litters/adult female 2012	0		9			1	
	1		10			2	
	2		9			1	
Recruited subadults	sum 2011	8	0	8	2	0	2
	spr 2012	0	0	0	4	1	5
	sum 2012	0	0	0	0	0	0
Dispersing subadults	sum 2011	3	3	6	0	0	0
	spr 2012	0	1	1	1	0	1
	sum 2012	0	0	0	0	0	0
Recruited adult	2012/13	5	6	11	0	3	3
Dispersing adult	2012/13	0	9	9	0	1	1

4.3.1.3 Survival and recapture estimation

An estimate of the variance inflation factor, $\hat{c} = 1.160$ ($p = 0.025$) was obtained using the saturated model $[\phi_{sex*site*time}, p_{sex*site*time}]$, by dividing the observed deviance of the model by the mean deviance of 1000 simulated models. The

saturated model did not violate the CJS assumption or suffer from critical lack of fit since $1 < \hat{c} < 3$. As the $\hat{c}$ value was significant the null hypothesis that $\hat{c} = 1$ was rejected and the variances in the model within Program MARK were adjusted accordingly. When recapture probability was stepped-down, the most parsimonious model was $[\phi_{sex*site*time}, p_{season-year}]$. The $\Delta QAIC_c$ between this model and the next most parsimonious $[\phi_{sex*site*time}, p_{season}]$ was 8.19 indicating that $p_{season-year}$ was the only recapture probability that should be considered. A similar step-down sequence was used to generate the model for adult survival and the most parsimonious model overall was retained $[\phi_{season}, p_{season-year}]$ (Table 4.3). This indicated that survival probabilities differed between summer (April-September) and winter (October-March) whereas recapture probabilities varied between summer, winter, and year. Models that contained sex or site effects on survival or recapture probabilities were not well supported ($\Delta QAIC_c > 14$) (Table 4.3).

Table 4.3 The ten most parsimonious Cormack-Jolly-Seber models of the candidate model set with the saturated CJS model.

The model used for parameter estimation is shown in bold. ϕ = survival probability; p = recapture probability.

	Model	$QAIC_c$	$\Delta QAIC_c$	No. Par.	QDeviance
1	**[ϕ(season), p(season-yr)]**	**902.602**	**0.000**	**6**	**595.126**
2	[ϕ(quarter), p(season-yr)]	903.884	1.283	8	592.283
3	[ϕ(season-yr), p(season-yr)]	904.042	1.441	8	592.441
4	[ϕ(quarter-yr), p(season-yr)]	906.446	3.844	10	590.684
5	[ϕ(time), p(season-yr)]	912.681	10.080	18	579.922
6	[ϕ(.), p(season-yr)]	916.229	13.627	5	610.803
7	[ϕ(sex), p(season-yr)]	917.383	14.782	6	609.908
8	[ϕ(site), p(season-yr)]	918.239	15.638	6	610.764
9	[ϕ(sex*site), p(season-yr)]	918.587	15.986	8	606.986
10	[ϕ(site*time), p(season-yr)]	931.702	29.101	31	570.050
CJS	[ϕ(sex*site*time), p(sex*site*time)]	1050.989	148.388	104	490.665

The annual estimate of squirrel survival was calculated from the product of the estimates of summer(ϕ) and winter(ϕ) each raised to the fifth power (five sampling occasions in each season per year; Table 4.4 and Appendix 2). The annual recapture probability estimate for 2012 was derived from the product of the yearly seasonal p

estimates raised to the power of the number of trapping sessions over which each estimate pertained (Table 4.4).

Table 4.4 Parameter estimates for ϕ and p with associated standard error.

Annual survival = $(\text{summer}(\phi))^5 \times (\text{winter}(\phi))^5$. Annual survival SE was estimated using the delta method. Annual recapture = $(\text{winter2012}(p))^2 \times (\text{summer2012}(p))^5 \times (\text{winter2013}(p))^3$. The SE of the annual recapture estimate could not be calculated using the delta method.

Time period	Survival estimate	±SE
5 week (winter)	0.952	0.015
5 week (summer)	0.835	0.023
Annual (50 week)	0.317	0.047
	Recapture estimate	
5 week (winter 2011/12)	0.723	0.059
5 week (summer 2012)	0.759	0.031
5 week (winter 2012/13)	0.489	0.040
5 week (summer 2013)	0.879	0.051
Annual 2012 (50 week)	0.015	--

4.3.2 Comparative demography

Demographic information on 47 grey squirrel populations from 36 peer-reviewed papers, one peer-reviewed book chapter, and four completed Irish PhD theses fulfilled the selection criteria (Table 4.5). Of these populations, 25 were situated in four distinct regions outside of the native grey squirrel range and two were clearly defined as frontier populations in addition to the two populations examined in the current study. The majority of studies collected data on grey squirrel populations located within deciduous habitat (n=33). Mean values for density, survival rate, breeding rate, and body mass (Figure 4.5) were available for most habitats and regions though, data pertaining to litter size, juvenile recruitment, and home range size were more sparse.

Table 4.5 Mean demographic values of grey squirrel populations in deciduous, mixed and coniferous habitat in four introduced regions and the native range.

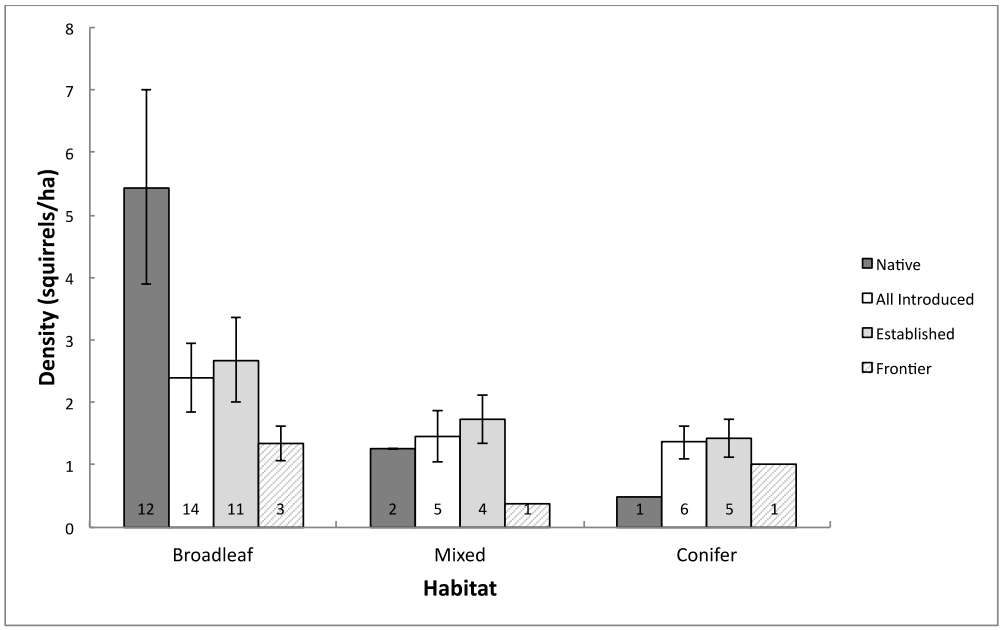
Unless otherwise specified values pertain to adults of both sexes (J: juvenile; F: female; M: male). Definititions for age groups follow the definitions given in the relevant source. More detail in Appendix 3.

Region	Habitat	No. of studies/ sites	Frontier or established	Density (sq./ha)	Survival rate %	Breeding rate %	Litter size (weaned)	Recruitment (J) %	Home range size (ha)	Body mass (g)
CP	Deciduous	N=1	F	1.14	31.7±4.7	67.9				580.5±6.8 (F) 551.5±6.7 (M)
KM	Mixed	N=1	F	0.38	31.7±4.7	75				625.6±10.6 (F) 565.8±11.3 (M)
Ireland[a]	Deciduous	N=4	E	2.24	36-52.9 0-46.9 (J)	63			2.46 (F) 1.33 (M)	594.7 (F) 561.2 (M)
Ireland[b]	Mixed	N=1	E	1.7		25.6			0.397-0.413 (F) 0.329-1.704 (M)	607.7 (F) 606.9 (M)
Ireland[c]	Conifer	N=1	E	0.95		62.5			6.58±3.15 (F) 1.95±0.15 (M)	655.55±24.22 (F) 564.95±30.93 (M)
UK[d]	Conifer	N=1	F	1.0	58.5	70		41		
UK[e]	Deciduous	N=7	E	2.93	55.75 38.2 (J)	56	1.22		3.17	600.5
UK[f]	Mixed	N=1	E	2.2						
UK[g]	Conifer	N=6	E	1.15	48.3 26 (J)	57			.89	579 (F) 577 (M)
Italy[h]	Deciduous	N=1	F	1.45	66	93	2.0	74.3	3.7 (F) 4.5 (M)	549
Italy[i]	Deciduous	N=1	E						2.69 (F) 4.13 (M)	
West Canada[j]	Deciduous/ Mixed	N=1	E	1.94			1.5			562.5 (F) 594.2 (M)

West Canada[k]	Conifer	N=1	E	2.54		77				603.7 (F) 608.6 (M)
Native Range[l]	Deciduous	N=18	E	4.49	44.1 34.7 (J)	69.45	2.12	47	1.97	554.9
Native Range[m]	Mixed	N=1	E	1.26	52 26 (J)		2.28			
Native Range[n]	Conifer	N=1	E	.49						

Separate means for females, males and juvenile are indicated by the letters F, M, and J respectively. [a] Lawton (1999), O'Teangana (1999), Lawton and Rochford (2007), McGoldrick (2011), Sheehy (2013). [b] Lawton (1999), Lawton and Rochford (2007). [c] O'Teangana (1999). [d] Wauters *et al.* (2000). [e.] Kenward (1985), Kenward and Parish (1986), Kenward and Tonkin (1986), Fitzgibbon (1993), Kenward and Holm (1993), Gurnell (1996), Kenward *et al.* (1998). [f] Kyle (2009). [g] Kenward and Hodder (1998), Kenward *et al.* (1998), Lurz and Lloyd (2000), Bryce *et al.* (2001), Gurnell *et al.* (2004a). [h] Gurnell *et al.* (2001). [i] Wauters *et al.* (2002). [j] Robinson and Cowan (1954). [k] Hwang and Lariviére (2006). [l] Hibbard (1935), Longley (1963), Nixon *et al.* (1967), Mosby (1969), Nixon and McClain (1969), Barkalow Jr *et al.* (1970), Doebel and McGinnes (1974), Montgomery *et al.* (1975), Nixon *et al.* (1975), Bouffard and Hein (1978), Thompson (1978a), Nixon *et al.* (1980), Brown and Batzli (1985), Gorman and Roland (1989), Fischer and Holler (1991), Koprowski (1991), Tounzen *et al.* (2012). [m] Fischer and Holler (1991), Healy and Welsh (1992). [n] Fischer and Holler (1991).

4.5a



4.5b

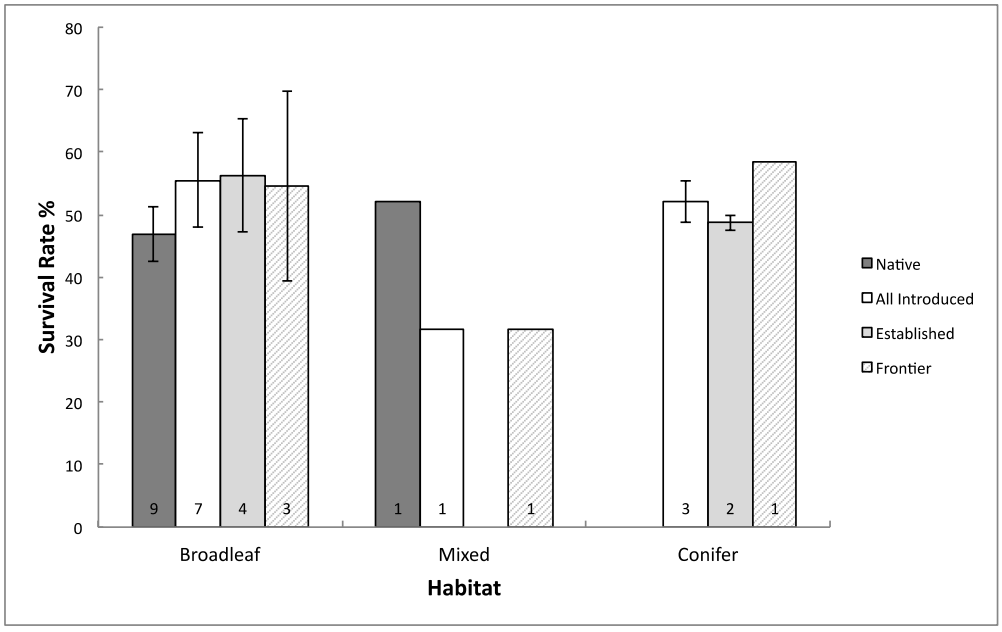
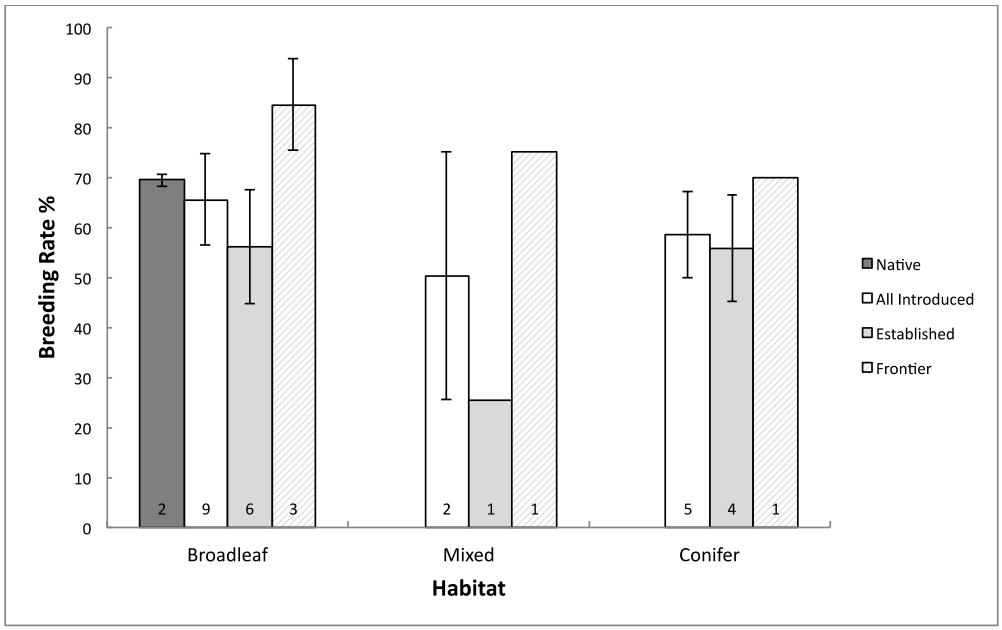


Figure 4.5 Mean values (± standard error) of grey squirrel a) population density, b) survival rate in populations across the native and introduced range of the animal as reported in the published literature. The means are separated by habitat and by population type; native (dark grey), all introduced (white), established introduced (light grey), and frontier introduced (grey hatching). The number of studies (n) from which the data for each population/habitat category are drawn is shown inside each bar. The data are also shown divided by region in Table 4.5 and by study in Appendix 3.

4.5c



4.5d

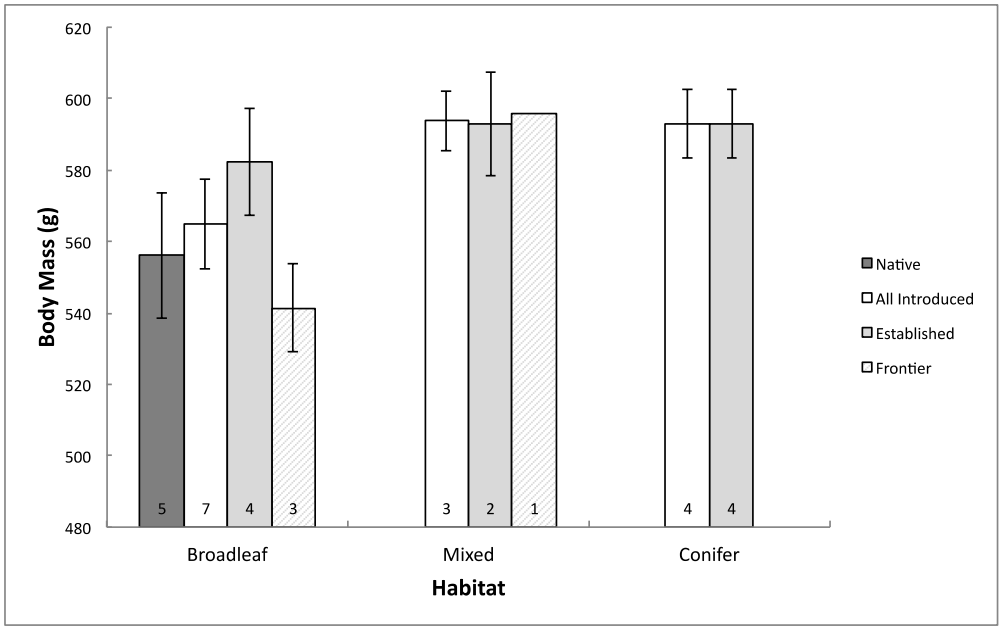


Figure 4.5 cont. This page and the previous: mean values (± standard error) of grey squirrel c) breeding rate, and d) body mass in populations across the native and introduced range of the animal as reported in the published literature. The means are separated by habitat and by population type; native (dark grey), all introduced (white), established introduced (light grey), and frontier introduced (grey hatching). The number of studies (n) from which the data for each population/habitat category are drawn is shown inside each bar. The data are also shown divided by region in Table 4.5 and by study in Appendix 3.

4.4 Discussion

This field study provides the first demographic information from frontier grey squirrel populations on the island of Ireland. Recorded grey squirrel densities in established populations vary according to habitat but are generally found to range between 2-6 squirrels ha^{-1} in broadleaf habitat and 1-2 squirrels ha^{-1} in mixed habitat across the native and introduced range. However, at the southern grey squirrel invasion frontier in Ireland, two populations with much lower densities were identified through a live trapping programme. Data from frontier populations are important as these populations could become established after a brief time depending on invasion dynamics. A broad scale comparison of trends in the demographic parameters of frontier and established populations across the native and introduced range is now possible. Such a comparison lays the groundwork for gaining a greater understanding of how newly established populations of terrestrial vertebrates evolve as range expansion and the invasion frontier proceeds through the landscape.

4.4.1 Variation in dynamics, survival, and recapture at the Irish grey squirrel frontier

Although habitat, seasonal, and weather variables can influence trapping success (Perry *et al.* 1977), grey squirrels are often readily trappable given appropriate equipment and bait. In the Irish frontier sites grey squirrel trapping success was high after the initial acclimatization period. The mixed habitat site (KM) supported a smaller number of significantly larger and heavier squirrels, though these animals were not in better condition than their counterparts, in the more densely populated deciduous site. As observed in many populations across the native and introduced range (Nixon and McClain 1969; O'Teangana 1999; Lurz and Lloyd 2000; Lawton and Rochford 2007), female squirrels in both sites were significantly larger, heavier, and in better body condition than males in the Irish frontier sites. Grey squirrels are not sexually dimorphic (Steele and Koprowski 2001); therefore it is likely that the greater mass often observed in females is related to weight gain during gestation

(Gurnell *et al.* 2008a; Sheehy and Lawton 2014). Population dynamics in grey squirrels are tightly tied to food resource availability, which varies seasonally and yearly (Nixon and McClain 1969; Koprowski 1991; Gurnell 1996). In the current study tree seed resource quality declined from good to poor between the autumn 2011 and 2012 seed crops in both study sites. A subsequent decline in squirrel density, breeding rate, and recapture probability was observed in the 2012/2013-winter season and following spring.

Survival of adult grey squirrels varied seasonally at the invasion frontier, with 5-weekly winter survival (October – March) higher than summer survival (April – September). This result is in contrast to values found for seasonal adult red squirrel survival by Wauters *et al*. (2008) who found summer survival rates to be ≥ winter survival rates in alpine Italian forested sites. However, it is typical for populations of Holarctic tree squirrels in temperate woodlands to exhibit higher survival in winter than in the summer season (Wauters *et al.* 2004; Vander Haegen *et al.* 2013). The observed difference in seasonal survival rates in this study was not due to the somewhat arbitrary, though meteorologically meaningful, definitions of the winter (October – March) and summer (April – September) seasons. Model 2 (Table 4.3), although not the most parsimonious model, produced estimates of ϕ that varied quarterly ($\phi_{\text{Jan-Mar}}$ = 0.96, $\phi_{\text{Apr-Jun}}$ = 0.87, $\phi_{\text{Jul-Sept}}$ = 0.81, and $\phi_{\text{Oct-Dec}}$ = 0.92) and maintained the trend of higher winter survival. As in other capture-mark-recapture studies on open populations the survival parameter was affected both by mortality and dispersal from the trapping area (Lebreton *et al.* 1992; Wauters *et al.* 2008). Young grey squirrels of approximately 8-10 months in age disperse during two distinct periods during the year (April – May and July – October) depending on the season of their birth (Thompson 1978a). Although subadult squirrels were excluded from survival and recapture analysis in this study, it is likely that adult squirrels could show limited dispersal tendencies that echo the movement patterns of younger animals and result in lower summer survival rates. Interestingly, survival estimates of subadult western grey squirrels (*S. griseus*) were not shown to be significantly different from adults (Vander Haegen *et al.* 2013), though it is unknown if the same would be found in eastern grey squirrel populations. The recapture estimates of adult

grey squirrels were generally high (≥ 0.7), did not differ between sites, and compared well with red squirrel recapture rates (Wauters *et al.* 2008), except for the estimate for the winter period between October 2012 and March 2013 inclusive, when it was much lower (Table 4.4). This period of low recapture probability directly corresponds to the period during which the lowest squirrel density was found in each site (Figure 4.3) after the sparse autumn 2012 tree seed crop. Previous studies have noted that grey squirrels are more difficult to capture in the summer and autumn due to natural food availability (Perry *et al.* 1977; Gurnell 1996) though, such observations are not supported by the recapture estimates of the current study.

4.4.2 Comparative demography

In Ireland, the grey squirrel invasion has progressed more slowly (1.94 km yr^{-1}; O'Teangana *et al*. (2000a)) than in the UK (7.66 km yr^{-1}; Okubo *et al*. (1989)) and faster than the more recent invasion in Italy (0.33-0.65 km yr^{-1}; Bertolino *et al*. (2014)). Red squirrel populations have declined in places where they co-occur with the introduced squirrel species in Europe. The most detrimental effects on red squirrel populations have been recorded in Britain while the damage to native Irish squirrel populations has been less severe, with the native species retaining a widespread but patchy distribution (Chapter 2; Carey *et al*. (2007)). Local red squirrel population extinctions in Italy, caused by grey squirrel presence, are predicted to worsen as the invasion in this country becomes more extensive, due to an increasing rate of spread (Bertolino *et al.* 2014). The synthesis of demographic parameters from grey squirrel populations in the well-studied European introduction regions and those from the native range and the less-studied introduction area of western North America, with examination of the ensuing trends, should bring valuable knowledge. Likewise, within-habitat comparisons of demographic parameters from native populations and introduced populations that are established or on the frontier will bring understanding to the differences in dynamics between such population types.

The vital statistics of species populations are not fixed and change in response to variation in external or internal conditions such as climate change, resource availability, competition, predation, landscape connectivity or inbreeding (Mills and Smouse 1994; Meserve *et al.* 1995; Creel *et al.* 2007). Disparities in population demography and dynamics between introduced, invasive, established, frontier, and native regions point to intrinsic differences in local ecological communities. Such differences may be related to the susceptibility of regions or habitats to invasion by a particular species. Scientists have long sought clues to explain community invasibility (Lonsdale 1999; Mack *et al.* 2000; Davis *et al.* 2005) though most experimental work has focused on plant systems. Biological invasions by the grey squirrel, which have varied in success, can be compared through the persistence, spread, or demographic profile of the species in each location. This measurable variation in invasion success provides an indication of corresponding variation in the invasibility of these regions. Armed with this information, landscape managers can respond more effectively to contain current and future species invasions.

Population density was the most commonly reported demographic parameter in the collected grey squirrel literature, with values available from 39 of 47 populations (Table 4.5, Figure 4.5a). In line with previously reported habitat preferences (Koprowski 1994), grey squirrel densities were higher in deciduous habitat than in mixed or coniferous forested landscapes across all regions and population categories. In mixed and coniferous habitats, introduced grey squirrel population densities were found to be higher than native population densities. The observation of higher squirrel densities in suboptimal habitat outside of the native range may indicate either a shortage of available ideal habitat for squirrel populations or that these habitat types are more habitable to grey squirrels outside eastern North America. Mixed and coniferous habitat also supported populations of heavier squirrels across all categories of populations than did deciduous habitat (Figure 4.5d). It is likely that body mass is inversely correlated to density through reduced intraspecific competition. Among introduced grey squirrel populations, established sites on average supported more dense populations than frontier sites. It is likely that grey squirrel populations at frontier sites were below carrying capacity at the time of

study due to recent colonization by the species. This pattern was upheld within individual European introduction regions, with the densities of frontier populations in Ireland and Britain observed to be lower than established populations, in similar habitats within the same region, although no comparison was possible for Italian squirrel populations. Indeed, the density values recorded in Irish frontier populations were lower than the mean densities recorded in similar habitats elsewhere within the introduced and native range. The maximum recorded mean grey squirrel densities within introduced populations were found in Britain, which were only exceeded by native-range populations in deciduous habitat. High densities of introduced grey squirrels extant in Britain could partially explain why the severest negative consequences of invasion have been reported in this country, such as elevated levels of bark-stripping damage (Kenward 1989; Mayle *et al.* 2009), disease transmission (Gurnell *et al.* 2006), and red squirrel decline (Gurnell and Pepper 1993).

The demographic parameter of survival rate, as with density, was most commonly reported from grey squirrel populations located in deciduous woodland (Figure 4.5b). In deciduous habitat the survival of grey squirrels was higher in introduced populations than in native populations, though the opposite was true in mixed habitat. Frontier introduced populations showed a higher survival rate only in coniferous habitat compared to established introduced populations. Within individual introduced regions differences between survival rate of established and frontier populations were inconsistent. Frontier adult annual survival rate in Irish frontier populations was lower than in established population areas, though the opposite trend was reported for British populations. A lack of published survival rates for established grey squirrel population in Italy prevented comparison between population categories in this region. Additionally, the survival rate in British populations is higher than in populations situated within the native range of the grey squirrel. Survival rate in open populations can be raised through both lower mortality and emigration rates. The high rate of grey squirrel spread recorded in Britain (Okubo *et al.* 1989) does not support that high annual survival could be caused by low population emigration in this region. Higher annual survival, through low mortality rates, likely act to increase local population densities and increase

juvenile emigration from saturated populations, leading in turn to higher spread rates in Britain compared with other introduction regions.

Breeding rates were only available for deciduous habitat from native populations and were higher than breeding rates from introduced populations overall but not from frontier populations alone (Figure 4.5c). The breeding rates of adult squirrels in frontier populations were among the highest observed when compared with mean values from established populations throughout the native and introduced ranges in all habitat types. The single study located on the invasion frontier in Britain reported a breeding rate from coniferous habitat (70%; Wauters *et al*. (2000)) that was comparable with those found in the current study from deciduous and mixed frontier sites in Ireland (67.9% and 75% respectively), though demonstrably lower than the rate recorded for a deciduous frontier site in Italy (86-100% over two years; Gurnell *et al*. (2001)). Given the trend that grey squirrel demographic parameters, such as density and survival, are higher when the species is located in optimal deciduous habitat; it is likely that grey squirrel frontier breeding rates in Britain are much higher in deciduous or mixed woodland sites than the 70% observed in coniferous habitat. The realistic potential for a very high breeding rate on the invasion frontier across all woodland habitats in Britain further explains the high geographic spread rate, especially in combination with high annual survival, which would force a greater percentage of juveniles to emigrate in order to successfully establish home ranges.

Further study of grey squirrel demographic parameters in all habitats, across the native and introduced range of the species, which would enable comparative statistical and quantitative methods to be employed, would strengthen conclusions drawn on demographic trends. In this qualitative comparison some of the conclusions were drawn based on single studies within a region or habitat and could be strengthened significantly if more demographic datasets were available. A further weakness, inherent in any comparative study, resulted from the specificity of demographic values to each population during the period of study, which are the product of local habitat, food resource, and climate conditions. Furthermore, the live

trapping studies included in Table 4.5 ranged greatly in length from a few months to 10 years, making quantitative comparison difficult.

4.4.3 Synthesis

The hypothesis that differences in the impact and scale of grey squirrel invasions would be reflected in the demographic profiles and dynamics of regional invasions is supported by this qualitative comparison of grey squirrel populations across the native and introduced range of the species. Population density, survival and breeding rates are closely intertwined and together form the basis of how each population functions. Taken together and separately, these demographic parameters each help to explain why the significant ecological and economic costs, such as disease transmission, rapid red squirrel decline, and bark stripping damage, inflicted by grey squirrels are highest in Britain (e.g. Kenward and Parish (1986); Gurnell *et al*. (2004b); Sainsbury *et al*. (2008)) than in other regions of the invasion. Differences in demography between regions are clues that point to variability in the invasibility or the invading population of each region. Woodland habitat extent, composition, and connectivity undoubtedly play a major role in grey squirrel demographic variation between introduction regions. Extensive and well-connected deciduous forest cover is found in England (Smith 2001) and other areas of Britain (Smith and Gilbert 2003) where grey squirrels are found. This is in contrast to the situation in Ireland, where forest cover is patchy and dominated by conifer species (Anon. 2007; Ní Dhubháin *et al.* 2009), and northern Italy, where the habitat consists of agriculture, unsuitable tree species and overall limited suitable squirrel habitat (Signorile and Evans 2007). Furthermore, the incidence and transmission of squirrelpox virus, which contributed to the decline of red squirrels in Britain (Tompkins *et al.* 2003; Gurnell *et al.* 2006; Sainsbury *et al.* 2008), is likely exacerbated by high grey squirrel population density there (Rushton *et al.* 2000). This disease, which is fatal to red squirrels, was absent, dormant or unobserved in Ireland until recent times (McInnes *et al.* 2013) and remains undetected in Italy (Gurnell *et al.* 2006). Across the introduced range of grey squirrels frontier

populations are distinct from established populations, in that they exhibit signs of population increase, rather than maintenance, through high breeding rates and low densities.

Improved understanding of the demographic structure of populations of invasive animals can lead to more targeted management and potentially more efficient responses to new invasion frontiers. The functional population structure of invasive species is an important resource for population biologists studying the mechanisms by which species expand their ranges. Species range alteration is predicted to increase as climatic changes accelerate (Parmesan 2006) and appropriate management responses to this phenomenon will be required. Warmer and drier conditions, predicted under climate change models, are thought to favour further spread and assist establishment of future grey squirrel introductions (Di Febbraro *et al.* 2013). It is likely that enhanced knowledge of population demographics at invasion frontiers could also be used to improve the success rate of reintroductions that are performed for species conservation objectives, which require a thorough understanding of demography (Converse *et al.* 2013). The trends examined here show that there is useful information to be gained from the demographic comparison of frontier and established populations of the invasive grey squirrel. Future management regimes would benefit from evidenced-based design, which incorporates the observed demographic differences between different habitat types, as well as established and frontier population categories.

Chapter 5 –

Invasion of a fragmented landscape: future range expansion and alternative management strategies for the invasive grey squirrel

Inserting a microchip (PIT tag) to uniquely identify the squirrel

Abstract

Biological invasions are an increasing threat to ecosystems worldwide. Effective management of an invasive species requires in depth knowledge of the invader, the invaded ecosystem, and their interactions. The complexity of the interactions between species and system can be reduced and represented in ecological models for better understanding. Here, the invasion of the fragmented landscape of Ireland by the eastern grey squirrel (*Sciurus carolinensis*) was represented in a spatially explicit population model. This species causes economic damage by bark stripping cultivated forest crops and is associated with population and range decline of the native red squirrel (*S. vulgaris*). The model was developed using estimates from the published range of demographic parameters and matched against the initial range expansion from the introduction of twelve squirrels in 1911 to the first recorded distribution in 1968. The two best fitting models were used to forecast the future dynamics of grey squirrel abundance and range in the southern region of Ireland under three different control strategies; culls, habitat modifications, and immunocontraceptive vaccination programmes, in addition to the absence of control. Region-wide intensive and coordinated culls were predicted to have the greatest impact on grey squirrel populations but with recovery beginning on the cessation of control. Control strategies consisting solely of immunocontraceptive vaccines, often preferred by public interest groups, were predicted to be ineffective. Complete eradication of the grey squirrel from Ireland is not feasible and strategic evidence-based management is required to limit further range expansion. Ecological models, such as those considered here, can be used to choose between informed management strategies and intensities based on predicted outcomes.

5.1 Introduction

Effective management of populations and landscapes requires an understanding of past events, the current circumstances, and likely scenarios for the future. The complexity of these issues in ecological systems often necessitates the use of mathematical models in which a simplified version of the real world can be created and manipulated. Such ecological models afford researchers valuable opportunities to gain insight into biological and ecological processes such as disease spread (LaDeau *et al.* 2007), change in habitable range (McDonald and Brown 1992), dispersal or invasion speed (Caswell *et al.* 2003), species interactions (Stenseth *et al.* 1997), effects of management or harvesting regimes (Taylor *et al.* 1987), and metapopulation patch occupancy (Hanski 1994). The development of spatially explicit population models (SEPMs), which combine landscape structure with metapopulation dynamics, has allowed for the incorporation of complex landscape/species interactions in models which consider species abundance, spatial distribution, and population viability (Dunning *et al.* 1995). This class of models is useful not only for researchers and managers concerned with future scenarios for endangered, threatened, or exploited species (Sachot and Perrin 2004; Rushton *et al.* 2006; Southwell *et al.* 2008) but also for those addressing the problems caused by expanding or invasive alien species (Kolar and Lodge 2002). Biological invasions now threaten biodiversity and ecological processes as well as agricultural and transport systems at both local and global scales (Vitousek *et al.* 1997; Mack *et al.* 2000). It is economically, ethically, and environmentally beneficial to address biological invasions early to minimize negative consequences (Mack *et al.* 2000; Myers *et al.* 2000; Bertolino and Genovesi 2003; Simberloff 2003). However, if species invasions proceed past the point of easy eradication then SEPMs can assist managers and researchers in making predictions about future abundance (Meekins and McCarthy 2002), or range extent (Higgins *et al.* 1996) and the effectiveness of control regimes (Vuilleumier *et al.* 2011).

The introduction and expansion of grey squirrels outside of their native range, and their effects on native species, is arguably one of the best scientifically documented

cases of biological invasion (Gurnell *et al.* 2006). Additionally, the ecologies of the grey squirrel in native and introduced areas and that of the European red squirrel (*Sciurus vulgaris*), the native squirrel most often affected by the invader, are well known (Koprowski 1994; Lurz *et al.* 2005). Many theoretical models supported by the in-depth knowledge of the dynamics of these species have been put forward over the recent decades. An early modeling paper (Okubo *et al.* 1989) used diffusion-reaction equations to examine the effects of competition with the native red squirrel on speed of grey squirrel spread. The question was again addressed, this time within a spatial context, by Rushton and colleagues (1997) by means of a bespoke SEPM. This original work led to many research collaborations, often using related models, that examined disease and competition mediated interaction between the squirrel species (Rushton *et al.* 2000; Tompkins *et al.* 2003; Gurnell *et al.* 2006; Sainsbury *et al.* 2008), future grey squirrel spread in Britain and Europe (Lurz *et al.* 2001; Tattoni *et al.* 2006; Bertolino *et al.* 2008; Di Febbraro *et al.* 2013), effects of conservation actions for red squirrels (Rushton *et al.* 1999; Hale *et al.* 2001; Gurnell *et al.* 2002), and effects of grey squirrel control (Rushton *et al.* 2002). Such bespoke models offer the advantage of being exquisitely tailored to the relevant system but suffer from limited wider appeal due to lack of transparency and incomplete replicability, which undermines the purpose of scientific publication. The high level of customization of bespoke models can often result in a lack of adaptability to other ecological systems and necessitate a higher level of mathematical and programming literacy than would otherwise be required among many conservation managers (Lurz *et al.* 2008). Recent advances in general population modeling software overcome many of the hurdles and difficulties of such individual models (Akçakaya and Root 2013) and allow for the formulation of standardised, transparent, and validated models that can be tailored to specific ecological systems through species specific demographic, ecological, and spatial parameters. Such models have facilitated the investigation of the population viability of tree squirrel introductions (Wood *et al.* 2007) and endangered populations of the Caucasian squirrel (*S. anomalus*) experiencing poaching and habitat fragmentation (Matsinos and Papadopoulou 2004) as well as range expansion and control options for the introduced red-bellied squirrel (*Callosciurus erythraeus*) in Argentina (Guichón and Doncaster 2008).

European countries have experienced both economic and ecological costs as a result of grey squirrel introductions. Damage to timber crops through bark stripping occurs mainly in the spring and summer months when squirrels strip the outer bark of pole stage hardwoods and consume the soft vascular tissue beneath (Lawton 2003; Mayle *et al.* 2009). Bark stripping behaviour appears to occur at greater frequency in the invaded woodlands of the United Kingdom and Ireland than in the native range (Kenward 1989) and may be a learned habitual behaviour acquired in youth during times of acute stress due to high post-breeding population levels and dispersal (Kenward and Parish 1986). Maximum estimates of the cost of grey squirrel tree damage at harvest are as high as £10 million in Britain and €4.5 million on the island of Ireland (Kelly *et al.* 2013). Alien grey squirrels are also blamed for the disappearance of red squirrels from many areas of Ireland, Britain, and Italy. Red squirrel replacement by grey squirrels is caused though a reduction in red squirrel juvenile recruitment levels where the species co-occur (Wauters *et al.* 2000; Wauters *et al.* 2001; Gurnell *et al.* 2004b) rather than through interference competition (Wauters and Gurnell 1999). The lack of recorded niche-partitioning behaviours (Wauters *et al.* 2002) and a greater digestive tolerance of tannin-rich, but nutritious acorns (Kenward and Holm 1993) also advantage the invader over the native. The transmission of the often-fatal squirrelpox virus from grey squirrel carriers to red squirrels has also been implicated in the rapid replacement of red squirrels in Britain (Tompkins *et al.* 2003; Sainsbury *et al.* 2008) and has recently been confirmed in Ireland (McInnes *et al.* 2013).

Early monitoring of the grey squirrel in Ireland, introduced in 1911, was irregular with the first distribution surveys undertaken in the second half of the 20th century, though the period between surveys has since decreased and methods have improved (Watt 1923; O'Teangana *et al.* 2000a; Carey *et al.* 2007). The expansion rate of the invasive squirrels has been measured, through consecutive distribution surveys, to be between 1.75 and 1.94 km yr^{-1} as the species has spread to the north and east coasts (O'Teangana *et al.* 2000a; McGoldrick 2011) and continues to expand to the south and south-west of the island (Chapter 2). Red squirrels, despite significant

recent declines, remain widespread in Ireland, though they are patchily distributed, and mainly confined to coniferous woodlands where they fare better than their congener (Chapter 2; Carey *et al*. (2007)).

The most effective invasive species control programmes require support, engagement, and funding at national and local levels from community, scientific, and governmental bodies (Mack *et al.* 2000; Bertolino and Genovesi 2003; Bryce *et al.* 2011). There is currently no coordinated grey squirrel control effort in Ireland. Gamekeepers or landowners typically carry out grey squirrel culls by trapping or shooting on a property-by-property basis. These culls are effective in the short term in reducing squirrel numbers and limiting bark stripping damage, but squirrel numbers recover to pre-cull levels within 2-3 months through dispersal from nearby uncontrolled woodlands (Lawton and Rochford 2007). Modifying the landscape by removing optimal habitat, impeding resource access, or reducing connectivity could delay future grey squirrel range or population expansion. Such management actions are difficult to implement over wide areas but might avoid ethical arguments related to fatal control measures (Bertolino and Genovesi 2003). The need to control overabundant wildlife in areas of high human habitation, where traditional control methods are inappropriate or undesired, has prompted research into wildlife fertility control, which acts to reduce birth rates rather than survival rates (Fagerstone *et al.* 2010). Early research into grey squirrel contraceptive methods focused on isolating sperm-specific antigens (Moore *et al.* 1997) but recent work in tree squirrels has achieved preliminary results through chemical interruption of reproductive hormone synthesis (Yoder *et al.* 2011; Mayle *et al.* 2013) and, more promisingly, through the induction of an immune response against gonadotropin-releasing hormone (Pai *et al.* 2011; Krause *et al.* 2014). Careful and unbiased examination of these control methods is needed to provide guidance for the design of grey squirrel management plans throughout the introduced range.

To this end advanced SEPM techniques were utilised to examine the population dynamics of the invasive grey squirrel in Ireland, where it has never before been spatially explicitly modeled. Retrospective modeling of the grey squirrel invasion

from the point of introduction to the first recorded distribution in 1968 ensured that this transparent and validated model was calibrated to this system. Uncontrolled grey squirrel population spread in the as yet un-invaded southwest region of Ireland was examined through forecast modeling. The effectiveness of alternative grey squirrel population management strategies was compared, over the short and long term, to ascertain which methods are best suited to reducing population numbers and delaying colonization of internationally valuable ecosystems. The strengths and weaknesses of this theoretical approach to invasive species control and management are highlighted and discussed.

5.2 Methods

5.2.1 Study area

The island of Ireland (84,421 km^2) encompasses the Republic of Ireland and Northern Ireland. The island is characterized by lush vegetation, a mild climate influenced by the warm water Gulf Stream Atlantic current, and annual rainfalls averaging between 1000 and 1400 mm yr^{-1} (Met-Éireann 2014). Land use is primarily agricultural and forest cover currently stands at approximately 10% and is increasing (Anon. 2007; Ní Dhubháin *et al.* 2009), though it remains highly fragmented. The study area for the retrospective modeling of the initial expansion of the grey squirrels consisted of approximately 18,000 km^2 in the Irish midlands (Figure 5.1), which encompassed the site of introduction and the first recorded distribution in 1968 (NPWS 1968). Future expansion and effects of control strategies were modeled over a similar area in the south of Ireland, where the grey squirrel continues to show range expansion (Figure 5.1). Killarney National Park (KNP; 102.89 km^2; 51°59' N 9°33' W), which contains oak and yew woodlands of international importance as well as many rare plant and animal species, was chosen as an example of a sensitive area at risk of grey squirrel invasion. This location, designated as a UNESCO biosphere reserve in 1982, provided a tangible and ecologically relevant basis for comparison of long-term outcomes of different control strategies on grey squirrel range expansion.

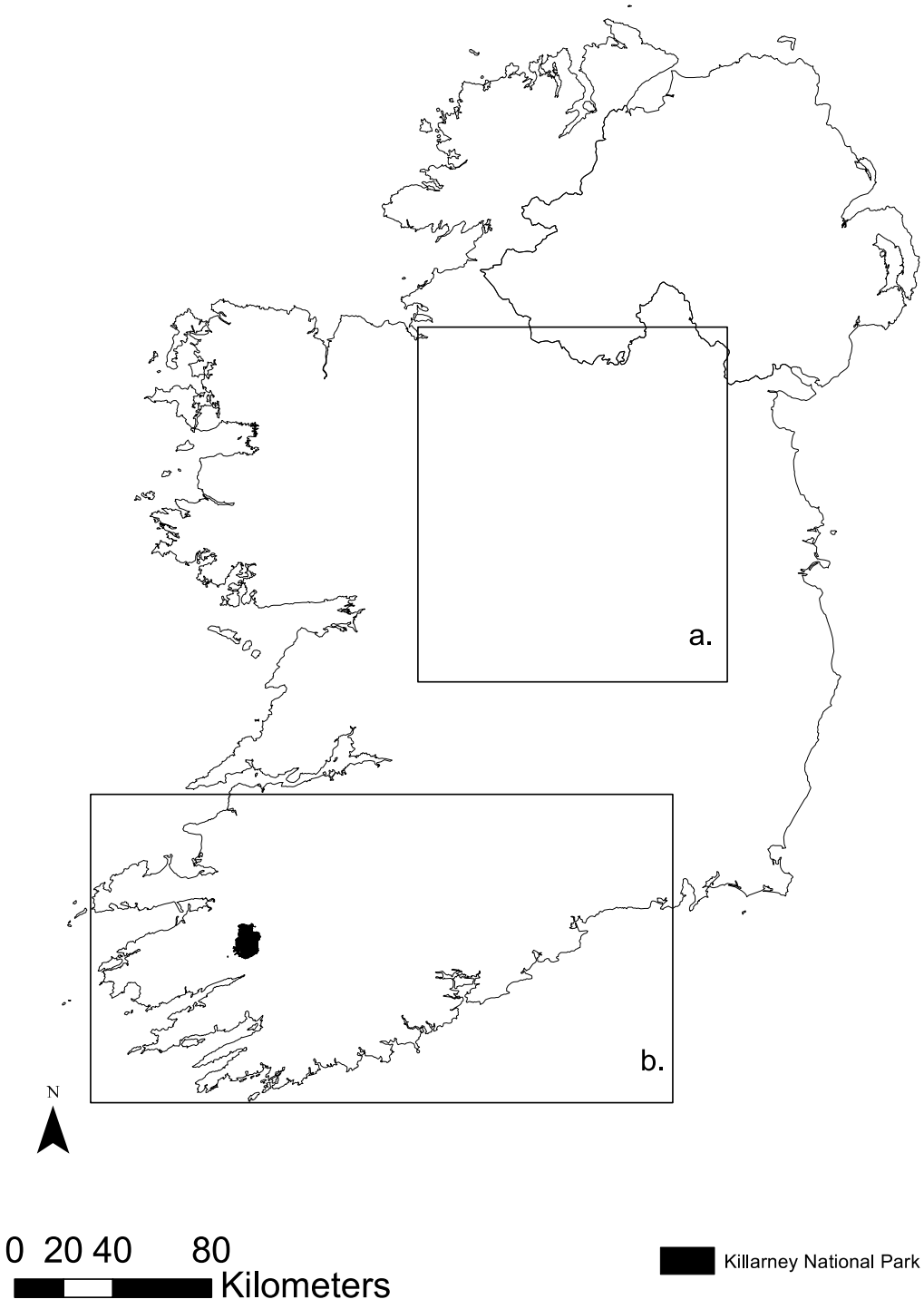


Figure 5.1 Map of Ireland showing a) the extent of the study region in the introduction area and b) the extent of the study area used to examine future expansion and control scenarios in the south and southwest of the country. Killarney National Park, which contains internationally valuable habitat and is vulnerable to grey squirrel invasion, is also highlighted.

5.2.2 The model

A spatially-explicit, stage-structured stochastic model was developed to simulate the past and future grey squirrel invasion on the island of Ireland. Life-history parameters and carrying capacities required for the model were drawn from published and previously collected data on the density and demography of introduced grey squirrel populations in Ireland, Britain, continental Europe, and from populations within the native North American range (Chapter 4). The model was created using the modeling software RAMAS GIS 6.0 (Akçakaya and Root 2013), which is designed to link metapopulation models with habitat data held in geographic information systems (GIS).

5.2.3 Habitat data and suitability

Several existing landscape datasets were consolidated and combined to create the habitat map used within the metapopulation model. The 2006 Corine Land Cover inventory (minimum mapping unit: 25 ha) for Ireland (EEA 2007) was supplemented with the 2007 Forest Inventory (FS 2007) and EPA Waterways (EPA 2003) data. The land cover types defined in these GIS datasets were dissolved into a limited number of habitats relevant to grey squirrels in ArcMap 10.0 (ESRI) and unions of similar habitats were created from each dataset. Three types of habitat suitable for grey squirrels were defined; broadleaf woodland, mixed woodland, and urban area as well as non-suitable matrix habitat which consisted of water bodies, bogs, agricultural land, and non-vegetated areas. RAMAS GIS 6.0 requires feature classes to be converted to a raster format. The raster had a cell size of 100 x 100 m.

Grey squirrels achieve highest population densities in broadleaf habitat in both their native and introduced ranges (chapter 4; Koprowski (1994)). Broadleaf woodland was assigned the highest suitability value within the model followed by mixed woodland. Elevated densities of grey squirrels have also been associated with high human densities in urban areas likely due to low predation rates and abundant food

resources (Bowers and Breland 1996; van der Merwe *et al.* 2005). Conifer woodland, which mostly exists as large plantation blocks in Ireland, is ecologically challenging for grey squirrels. This species is unable to manoeuvre effectively within the thin canopy branches to acquire the seed-bearing cones (Lurz and Lloyd 2000) that are energetically poorer than deciduous tree seeds. In Britain conifer woodlands tend to be sink habitats for grey squirrel populations and are sustained through immigration from nearby broadleaf areas (Lurz *et al.* 1995; Kenward *et al.* 1998). Consequently, in this model conifer woodland was considered as unsuitable matrix habitat.

RAMAS GIS 6.0 uses the definition of habitat patches suitable for grey squirrel populations to link habitat mapping and metapopulation modeling functions. Areas of habitat with a carrying capacity ≥ 1 squirrel ha^{-1} were defined as patch habitat and the surrounding non-suitable habitat as matrix habitat. Grey squirrels occupy non-exclusive home ranges, which vary in size between less than 1 ha to over 5 ha depending on food resources and population density (Kenward 1985; Lawton and Rochford 2007). Furthermore, routine extra-range exploratory movements across matrix habitat have readily been observed, especially in areas of highly fragmented woodland habitat (Gurnell 1987). A species' perceptual range is defined as the maximum distance at which the animal can perceive the existence of remote habitat patches (Zollner 2000) and is linked to both body mass and horizon height of the destination habitat (Mech and Zollner 2002). The perceptual range of the grey squirrel was measured empirically to be greater than 300 m (Zollner 2000) with an upper threshold of 400 m (Goheen *et al.* 2003). Furthermore, small areas of woodland habitat isolated by more than 500 m of matrix agricultural habitat from larger woodland patches are less likely to contain grey squirrels (Fitzgibbon 1993). Using these estimates of home range size, perceptual range, and exploratory movements areas of suitable habitat within 400 m of each other were grouped as a single "patch" for metapopulation modeling. The inter-patch distance was defined as the nearest edge-to-edge distance. The group of squirrels residing within each patch was termed a "population". The carrying capacity of each patch was the total habitat suitability, which was calculated as the sum of the habitat values of the woodland

and urban cells. Suitable habitat in Ireland is extremely fragmented at national and local scales. Smaller patches, with a carrying capacity (K) < 50 individuals, were treated as habitat fragments suitable for enhancing dispersal between larger populations. Including all suitable habitat patches would have expanded the patch matrix drastically and exceeded program limitations on number of populations. Focusing analysis on the major patches allows for conservative estimation of the invasion dynamics of this system.

5.2.4 Demographic data

The elements of an age-structured Leslie matrix with three age classes for each sex were estimated using empirically collected and previously published demographic and density data (Chapter 4). The age classes modeled were juveniles (0 – 1 year), yearlings (1 - 2 years), and adults (> 2 years) following the example of previous work (Guichón and Doncaster 2008). This Leslie matrix was applied to each population once every time step (year) within the metapopulation modeling program, which resulted in all demographic processes (births, deaths, immigration, and emigration) occurring discretely rather than continuously. The following assumptions were required to fit this type of model to the grey squirrel system; 1) all litters are produced in one period each year, 2) each subpopulation is censused before the annual birth pulse (pre-breeding census) and 3) no deaths occur between the census and the completion of reproduction in a time step.

Fecundity values for each stage compose the top row of an age-structured Leslie matrix while survival rates from the *i*th to the *j*th stage fill the sub diagonal and all remaining elements are zero. Placing the adult survival rate in the bottom right element of the Leslie matrix allows for individuals older than 2 time steps to be retained in the model in a composite adult age class. Annual survival is relatively constant once squirrels reach maturity (Gurnell 1987) making a composite age class grouping appropriate. Standard deviation matrices composed of elements equaling

5% of the corresponding element in the Leslie matrix were also created for each set of demographic inputs.

Fecundity values were derived from maternity rates using the following equation (Akçakaya and Root 2013):

$$F_{age\ class} = (\%\ breeding\ ♀) * (juvenile\ survival) * (litter\ size) * \left(\frac{litters}{year}\right) * (sex\ ratio)$$

As the average grey squirrel litter contains between two and four pups with a maximum of eight (Hibbard 1935; Nixon and McClain 1975; Koprowski 1994; Thorington Jr *et al.* 2012), every litter was assumed to consist of three pups. Juvenile female squirrels in their first year of life have rarely been observed to produce a litter, though such events have been recorded in Britain and North America (Shorten 1954; Smith and Barkalow 1967; Nixon and McClain 1975). For the purposes of calculating age class fecundity, it was estimated that 5% of juvenile females would produce one litter in the year of their birth. Yearling females were estimated to breed 75% of the time and to produce one litter year^{-1}, and 100% of adult females were assumed to produce two litters year^{-1} (Shorten 1954; Nixon and McClain 1975; Gurnell 1987). Such high rates of yearling and adult litter production were chosen after initial examination of a range of fecundity values and are justified by high breeding rates observed at invasion frontiers (Chapter 4). Fecundity values were varied by ± 25% of the value to account for uncertainty in estimation (Table 5.1). The sex ratio of young squirrels was 1:1 in the model in the absence of contradictory studies. Grey squirrels are polygamous and the care of the young is purely maternal. Each sex is capable of mating with more than one member of the opposite sex during a mating season (females may mate with up to eight males) (Koprowski 1992; Koprowski 1993; Steele and Koprowski 2001). In the model, male squirrels were permitted to breed with a maximum of six females, corresponding to the average overlap of male home ranges with female home ranges (Steele and Koprowski 2001).

Survival rates for juvenile and yearling/adult squirrels were estimated from values recorded throughout the native and introduced range of the species in the literature. Reported survival rates for juvenile squirrels vary widely from 18-70% during average or good years (Chapter 4; Appendix 3) and therefore a rate of 40% was chosen as the input value, which is close to the mean of reported values. Greater consensus surrounds the value of yearling and adult survival rates, which are often estimated to lie between 50-70% (Chapter 4; Appendix 3; Gurnell (1987); Wauters *et al*. (2000)). For this model the yearling and adult survival rates were set to 70% following poor performance of trial models with lower survival rates. Fast population increase and low intraspecific competition rates at the invasion frontier of a spreading species (Wauters *et al.* 2000; Gurnell *et al.* 2001) justify the choice of an adult and yearling survival rate at the upper end of the naturally observed range. The survival rates were varied by ± 25% of the value to account for uncertainty in these estimates (Table 5.1).

5.2.5 Dispersal

Within RAMAS, dispersal is defined as one-time movements between habitat patches rather than annual or daily movements (Akçakaya and Root 2013). As with the demographic processes, dispersal in the model occurred once annually at a rate dependent on the inter-patch distance and the age and sex of the disperser. The dispersal process was simulated using a negative exponential equation and a defined maximum value of the form:

$$Dispersal = ae^{\left(\frac{-D_{ij}{}^{c}}{b}\right)} \; if \; D \leq max$$

$$Dispersal = 0 \; if \; D > max$$

where *a*, *b*, and *c* are constants and *D* is the edge to edge distance between the *i*th and *j*th patches. It was possible with the above equation to manipulate both the mean and maximum dispersal distance of squirrels within the model. Average grey

squirrel dispersal distance is approximately 1 km (Gurnell 1987; Koprowski 1996), though adults have been reported to return to their home range from distances of 4.5 km (Hungerford and Wilder 1941). Consequently, mean and maximum dispersal distances were estimated at 1 and 5 km for the model respectively. To account for uncertainty in these estimates and in the creation of the habitat suitability map the dispersal values were varied by ± 50% (Table 5.1). Narrow hedgerows and treelines, which greatly enhance connectivity in the fragmented Irish landscape, were unable to be included in the patch map due to the 100 x 100 m pixel size resolution. The inclusion of a higher mean dispersal distance of 2 km and maximum dispersal distance of 9 km accounted for high habitat connectivity. As settled adults rarely shift home range, dispersal in grey squirrels is biased towards younger animals and males (Gurnell 1987; Gurnell *et al.* 2001). Exact ratios of dispersers are difficult to obtain experimentally as this varies by year and habitat. One study, however, recorded that 94% of male juvenile grey squirrels left the natal area compared to 63% of juvenile females (Koprowski 1996). Estimates of juvenile dispersal rate for the model were based on this research and were decreased for each sex by 50% for the yearling age class and similarly by a further 50% for the adult age class (Table 5.1).

5.2.6 Density dependence

The dependence of dispersal rates on population density or abundance can be important to the functional ecology of a species existing within a metapopulation. Different species of birds and mammals have been observed to alter dispersal patterns positively, negatively, or not at all in response to changing population density (Matthysen 2005). The incorporation of a small density dependent dispersal constant improved the fit of the *C. erythraeus* SEPM (Guichón and Doncaster 2008). The effect of including positive density dependent dispersal in this simulation was evaluated by running each model with and without the inclusion of this constant (Table 5.1). Including density dependent dispersal within RAMAS causes a greater proportion of individuals to disperse as source population density increases

(Akçakaya and Root 2013). Within-sex density dependence caused altered levels of reproduction, recruitment, emigration and survival in well-established populations of *S. vulgaris* (Wauters *et al.* 2004). Density dependence of all vital rates was included in the model where possible as "contest" competition in which resources are shared unequally among competing individuals and populations are assumed to recover from low densities (Akçakaya and Root 2013).

Table 5.1 Estimates of parameters used as model inputs for the spatially explicit population model designed to examine future grey squirrel (*Sciurus carolinensis*) expansion in Ireland. If a range of values was used these are shown in parentheses.

		Values (range)	
Parameter	Classification	Model trial A	Model trial B
Habitat Quality (K)	Broadleaf	2 squirrel ha^{-1}	
	Mixed	1.5 squirrel ha^{-1}	
	Urban	1 squirrel ha^{-1}	
	Matrix	0 squirrel ha^{-1}	
Survival rates	Juvenile	0.4 (0.3-0.5)	0.5 (0.375-0.6125)
	Yearling	0.7 (0.525-0.875)	0.7 (0.525-0.875)
	Adult	0.7 (0.525-0.875)	0.7 (0.525-0.875)
Fecundity rates	Juvenile	0.03 (0.0225-0.0375)	0.0375 (0.0281-0.0459)
	Yearling	0.45 (0.3375-0.5625)	0.5625 (0.4219-0.6891)
	Adult	1.2 (0.9-1.5)	1.5 (1.125-1.838)
Finite rate of increase (λ)		1.0646 (0.7985-1.3308)	1.1859 (0.8894-1.4672)
Mean dispersal distance		1 km (0.5-2.0)	
Max dispersal distance		5 km (2.5-9.0)	7.5 km (5-9.0)
♂ : ♀ relative dispersal	Juvenile	1 : 0.6	
	Yearling	0.5 : 0.3	
	Adult	0.25 : 0.15	
DDD* constant		0 (0.001)	
Competition type		Contest	

*Density dependent dispersal

5.2.7 Stochasticity

Demographic and environmental stochasticity were incorporated into the model at each time step in order that the model might more accurately reflect the true natural situation. Numbers of offspring were sampled from a Poisson distribution and numbers of dispersers from a binomial distribution to model demographic stochasticity and avoid the unrealistic occurrence of fractional numbers of individuals in the model (Akçakaya and Root 2013). Environmental stochasticity was accounted for in the model by randomly sampling the demographic rates from a lognormal distribution using means from the Leslie matrix and standard deviations taken from the standard deviation matrix (Akçakaya 2000; Akçakaya and Root 2013).

5.2.8 Validating the model

Validation trials of the model were performed in the introduction area surrounding the release site at Castle Forbes, Co. Longford (Figure 5.1) over the 57-year period between the release of grey squirrels in 1911 and the first distribution survey in 1968 (NPWS 1968). To find a model that adequately represented the invasion dynamics of the grey squirrel, three of the estimated input parameters (finite rate of increase (i.e. the eigenvalue λ of the stage matrix), mean dispersal distance, and maximum dispersal distance (Table 5.1)) were systematically varied as in Guichón and Doncaster (2008). A modified 3x3 Latin square was used to test three levels (low, medium, and high) of each input parameter with a balanced design. Mean dispersal distances of 0.5 and 2 km were always paired with the same demographic and maximum dispersal parameters, which resulted in 12 initial parameter input sets. Each parameter set was evaluated with and without density dependent dispersal on an approximately 18,000 km^2 extent of spatial landscape of identified patches located in the introduction region. Multiple other combinations of input parameters were examined to ensure that a model with better fit did not exist outside of the original Latin squares (total initial model runs = 17; model trial A in Table 5.1). The

model run for each parameter combination was run for 1,000 replications and 57 time steps ensuring that the initial population at the release site (Castle Forbes, Co. Longford) contained six each of adult male and female grey squirrels. The suitable habitat patches, classified by RAMAS, that existed within the 1968 range extent (NPWS 1968) were identified and the proportion of area matching between the observed historical range and each of the tested models was ranked using the simple matching coefficient (SMC). This metric is calculated as (a+b)/c, where a is the specific area of suitable habitat that was both observed and predicted to be occupied, b is the specific area of suitable habitat observed and predicted to be unoccupied, and c is the total area of suitable habitat identified within the introduction region. SMC proportions closer to 1 indicate higher spatial similarity between observed and predicted ranges. All matches were improved by prohibiting dispersal across the Shannon River, which flows to the immediate west of the release site and is anecdotally responsible for the absence of grey squirrels in the west of Ireland (Carey *et al.* 2007). As the best match was near the higher extremes of the set of tested models a further set of models in a similar Latin square arrangement with higher values for demographic rates and maximum dispersal distance (model trial B in Table 5.1).

5.2.9 Modeling the effects of population management strategies on future range expansion

Future squirrel expansion and control regimes were modeled in the southern region of Ireland, where the grey squirrel continues to expand its range, using the demographic and dispersal parameters that defined the two models that best matched the initial range expansion (Figure 5.1). Each model was used to predict the invasion outcomes under each control scenario over a period of 25 years with 1000 replications from 2012 when the southern range frontier was determined (Chapter 2). Patches within the invaded range in 2012 were set at carrying capacity with a stable age distribution derived from the Leslie matrix for the first time step of each control scenario. The total squirrel abundances and range extents that resulted from

two intensity levels of three distinct management actions: 1) proportional culls, 2) decreasing available resources, and 3) immunocontraception of females were compared for each model. Each management action was performed over two spatial extents: 1) all patches and 2) patches within a 20 km wide buffer zone preceding and behind the 2012 invasion frontier to examine the suitability and relevance of frontier based control programmes. Additionally, the effects of each management action were examined over a 200-year time period to predict average year of arrival in KNP. The effects of culls (performed yearly for five consecutive years), carried out near the beginning of the simulation (2013-2018) at high and low intensity levels (70% and 30% respectively of all adult and yearling squirrels removed during each year of the cull), were modeled at both spatial extents using the population management function within RAMAS. Resource reduction was simulated in two ways; first by removing all broadleaf habitat from the GIS landscape and second by decreasing the carrying capacity of each patch by 50%. The spatial dynamics subprogram of RAMAS was used to create temporal trend files and population management actions that simulated habitat modification. These actions were simulated within the model at the 2013 time step for all populations with K>25 to examine the effects of habitat modification at a finer scale. Finally, two immunocontraceptive vaccination programme scenarios were modeled. In these two programmes high and low (70% and 30% respectively) proportions of yearling and adult females were sterilized with a 100% effective vaccine for 5 years from 2013. The effects of these fertility control regimes on grey squirrel invasion dynamics were modeled by adjusting the relative fecundities of yearling and adult females to 30% and 70% of original values (for high and low levels of vaccination). Sterilization from this vaccine was assumed to be permanent but not to affect survival. It was assumed in the model that the effects of the vaccine on relative fecundity would taper off by 20% each year for 5 years from the cessation of the vaccination programme, as the proportion of vaccinated females should naturally decrease over time. It was necessary to modify the type of density dependence within the model for the immunocontraception scenarios from “contest” to “ceiling”, so that this function in RAMAS would not override the modified relative fecundities.

5.3 Results

5.3.1 Habitat suitability

In the introduction region surrounding the release site 465 patches of suitable habitat composing 506.64 km^2 or 2.8% of the c. 18,000 km^2 were identified (Figure 5.1, Figure 5.2). Each identified patch had a carrying capacity > 50 squirrels as was specified in the model design to limit complexity and achieve a conservative output. The area occupied by grey squirrels by 1968 as reported by O'Teangana *et al.* (2000a), included 103 of these patches and accounted for 114.07 km^2 or 22.5% of suitable habitat in the region. In the southern region, where control regimes and future expansion were modeled, 470 patches of suitable habitat occupied 595.6 km^2 of the available land area (c. 18,000 km^2). At the beginning of the control scenarios 126 patches were occupied at carrying capacity by grey squirrels, which accounted for 155.9 km^2 of suitable habitat (Figure 5.1).

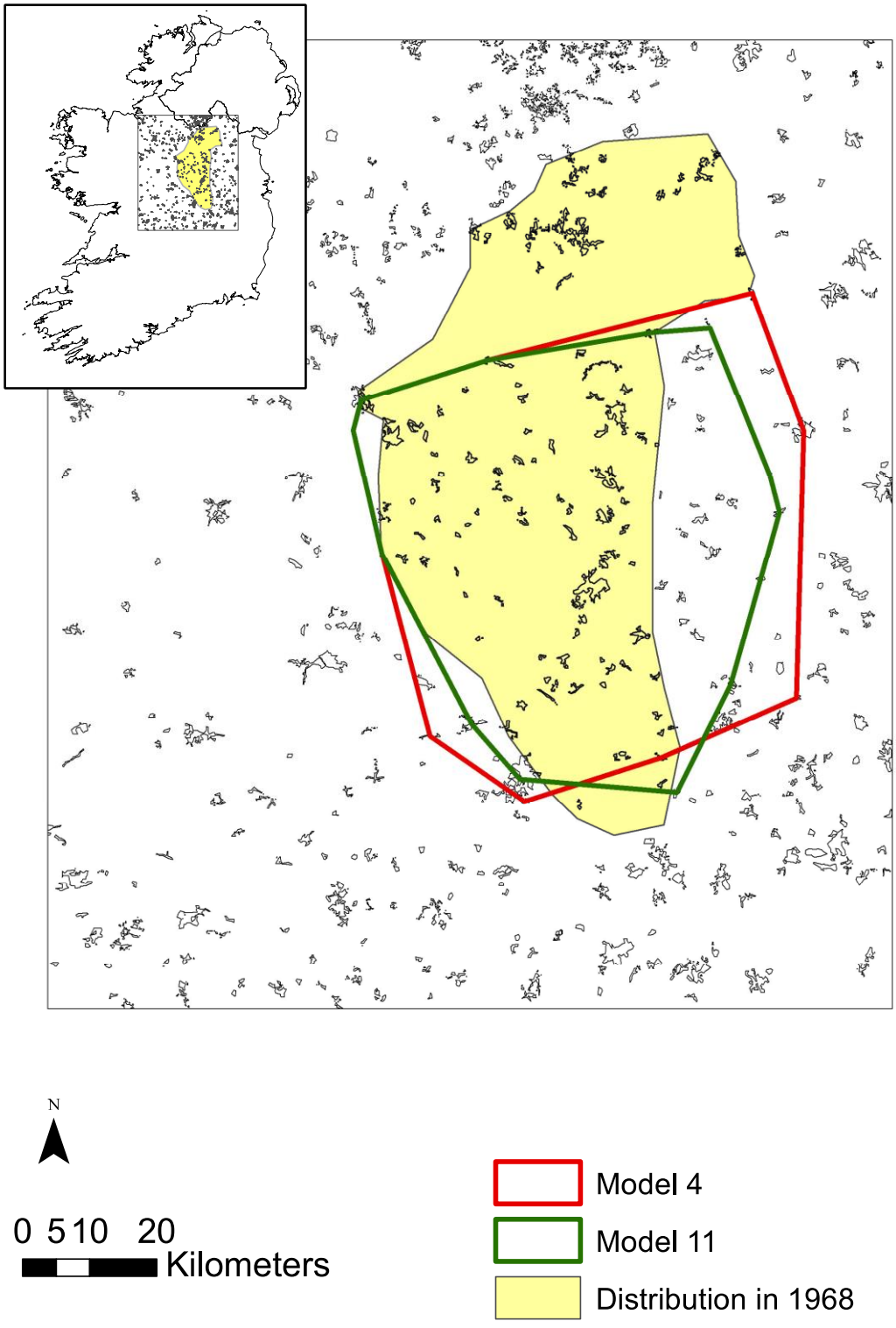


Figure 5.2 Map showing habitat patches suitable for grey squirrels (*Sciurus* carolinensis) in the Irish midlands. The grey squirrel invaded area in 1968 is shaded yellow and the minimum convex polygons of two models which most closely matched are shown in red (model 4; overestimate) and green (model 11; underestimate) for the year 1968.

5.3.2 Model validation

The inclusion of positive density dependent dispersal in the models did not consistently improve the match between observed and predicted patch occupancy. Indeed, in the majority of models the density dependent dispersal constant caused either no change to the SMC or a decrease in fit (Table 5.2). Good matching proportions (SMC $\geq$ 0.8) occurred in models with each value of population growth (λ) considered. Mean dispersal distances between 1 and 2 km and maximum dispersal distances of 7.5 and 9.0 km were also associated with good matches. Based on high matching proportions, models 4 and 11 (Figure 5.2) were chosen as the best representative models out of the 70 tested. Similar levels of overestimation (model 4; +6.3 km^2) and underestimation (model 11; -6.37 km^2) of the observed invaded suitable patch area guided the choice of these models though some others generated marginally better matches. Both models 4 and 11 included the same maximum dispersal distance of 7.5 km. None of the models tested predicted the presence of squirrels in the northern part of the 1968 range. Initially squirrel abundance increased gradually but was predicted to begin increasing at a faster rate approximately 20 years post release (Figure 5.3).

Table 5.2a Mmodel inputs, matching and area results for the Latin Square designs of model trial A parameter values (See Table 5.1).

The inputs that were varied in the design include the finite rate of increase (λ), mean dispersal distance (MeanDD), and maximum dispersal distance (MaxDD). The simple matching coefficient (SMC) ranks the absolute match between predicted and observed occupied patch area. The area predicted to be occupied by grey squirrels (with the difference from observed area in parentheses) 57 years after release. Models are shown first without and then with the inclusion of the density dependent dispersal constant.

Model run A						Density Dependent Dispersal	
	λ	MeanDD	Max DD	SMC	Area (km^2)	SMC	Area (km^2)
1	0.7985	0.5	7.5	0.743	29.35 (-84.72)	0.753	17.54 (-96.53)
2	0.7985	1	5	0.776	26.73 (-87.34)	0.776	26.73 (-87.34)
3	0.7985	1.5	2.5	0.741	13.06 (-101.01)	0.741	13.06 (-101.01)
4	**0.7985**	**2**	**7.5**	**0.850**	**120.37 (+6.3)**	0.831	92.61 (-21.46)
5	1.0646	0.5	2.5	0.741	13.06 (-101.01)	0.741	13.06 (-101.01)
6	1.0646	1	7.5	0.854	69.13 (-44.94)	0.854	57.9 (-56.17)
7	1.0646	1.5	5	0.776	26.73 (-87.34)	0.776	26.73 (-87.34)
8	1.0646	2	2.5	0.742	12.78 (-101.29)	0.742	12.78 (-101.29)
9	1.3308	0.5	5	0.762	21.39 (-92.68)	0.749	16.09 (-97.98)
10	1.3308	1	2.5	0.742	12.78 (-101.29)	0.742	12.78 (-101.29)
11	**1.3308**	**1.5**	**7.5**	**0.874**	**107.7 (-6.37)**	0.841	80.73 (-33.34)
12	1.3308	2	5	0.776	26.73 (-87.34)	0.776	26.73 (-87.34)
13	1.0646	1.5	7.5	0.837	92.13 (-21.94)	0.846	82.75 (-31.32)
14	1.3308	1	5	0.776	26.73 (-87.34)	0.776	26.73 (-87.34)
15	1.3308	1	7.5	0.863	73.15 (-40.92)	0.851	56.79 (-57.28)
16	1.3308	2	7.5	0.844	121.53 (+7.46)	0.868	108.53 (-5.54)
17	1.0646	2	7.5	0.832	124.22 (+10.15)	0.840	88.04 (-26.03)

Table 5.2b Model inputs, matching and area results for the Latin Square designs of model trial B parameter values (See Table 5.1).

The inputs that were varied in the design include the finite rate of increase (λ), mean dispersal distance (MeanDD), and maximum dispersal distance (MaxDD). The simple matching coefficient (SMC) ranks the absolute match between predicted and observed occupied patch area. The area predicted to be occupied by grey squirrels (with the difference from observed area in parentheses) 57 years after release. Models are shown first without and then with the inclusion of the density dependent dispersal constant.

Model run B						Density Dependent Dispersal	
	λ	MeanDD	Max DD	SMC	Area (km^2)	SMC	Area (km^2)
1b	0.8894	0.5	9	0.764	22.13 (-91.94)	0.755	18.58 (-95.49)
2b	0.8894	1	7.5	0.861	68.78 (-45.29)	0.853	58.75 (-55.32)
3b	0.8894	1.5	5	0.776	26.73 (-87.34)	0.776	26.73 (-87.34)
4b	0.8894	2	9	0.762	157.38 (-43.31)	0.785	143.93 (+29.86)
5b	1.1859	0.5	5	0.760	20.46 (-93.61)	0.753	17.82 (-96.25)
6b	1.1859	1	9	0.841	80.59 (-33.48)	0.841	65.06 (-49.01)
7b	1.1859	1.5	7.5	0.832	93.8 (-20.27)	0.858	79.88 (-34.19)
8b	1.1859	2	5	0.776	26.73 (-87.34)	0.776	26.73 (-87.34)
9b	1.4672	0.5	7.5	0.766	22.89 (-91.18)	0.755	18.53 (-95.54)
10b	1.4672	1	5	0.776	26.73 (-87.34)	0.776	26.73 (-87.34)
11b	1.4672	1.5	9	0.814	132.73 (+18.66)	0.794	107.28 (-6.79)
12b	1.4672	2	7.5	0.846	122.22 (+8.15)	0.834	93.39 (-20.68)
13b	1.1859	1	7.5	0.864	70.77 (-43.3)	0.851	56.79 (-57.38)
14b	1.1859	1.5	9	0.792	139.02 (+24.95)	0.785	109.68 (-4.39)
15b	1.4672	1	7.5	0.859	69.78 (-44.29)	0.853	58.69 (-55.38)
16b	1.4672	1	9	0.847	78.95 (-35.12)	0.850	63.08 (-50.99)
17b	1.4672	1.5	7.5	0.874	106.67 (-7.4)	0.846	81.82 (-32.25)
18b	1.1859	2	7.5	0.859	114.02 (-0.05)	0.826	93.27 (-20.8)

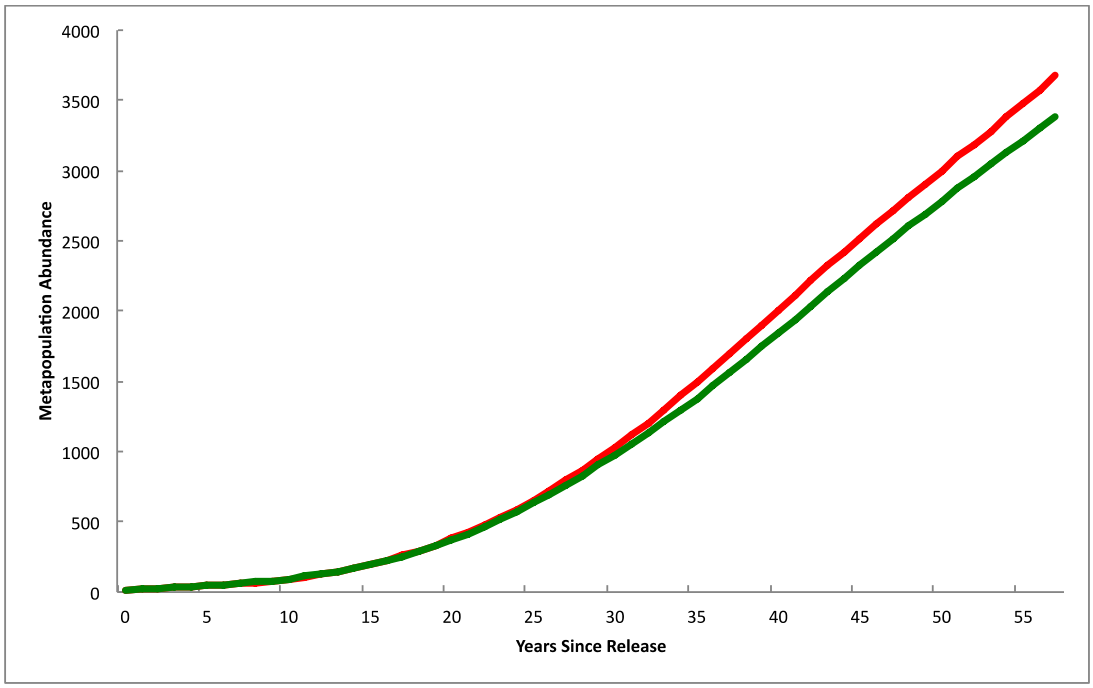
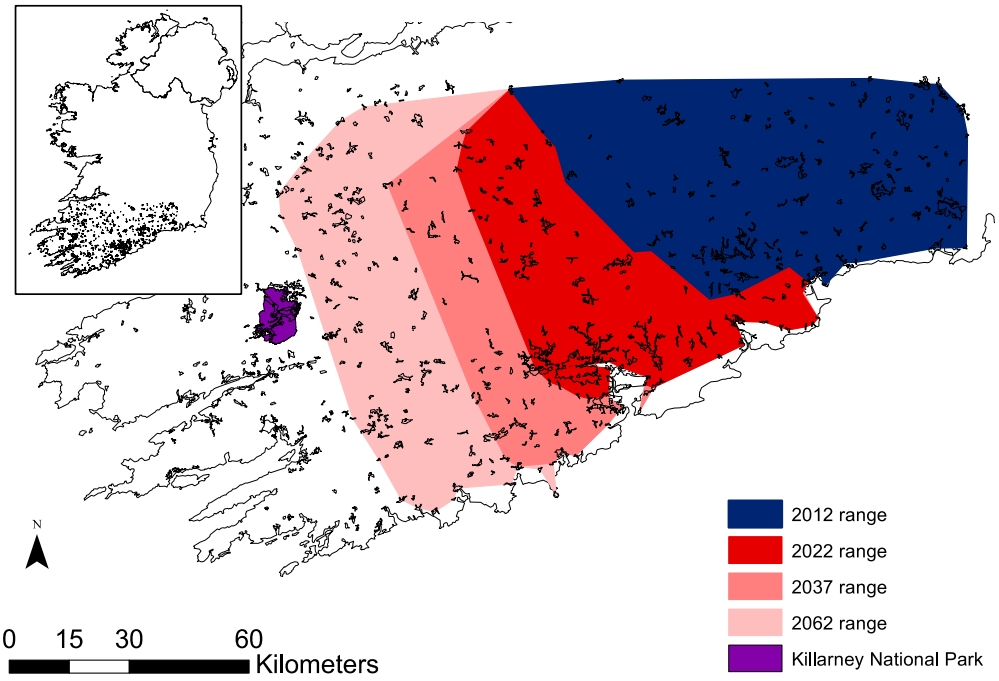


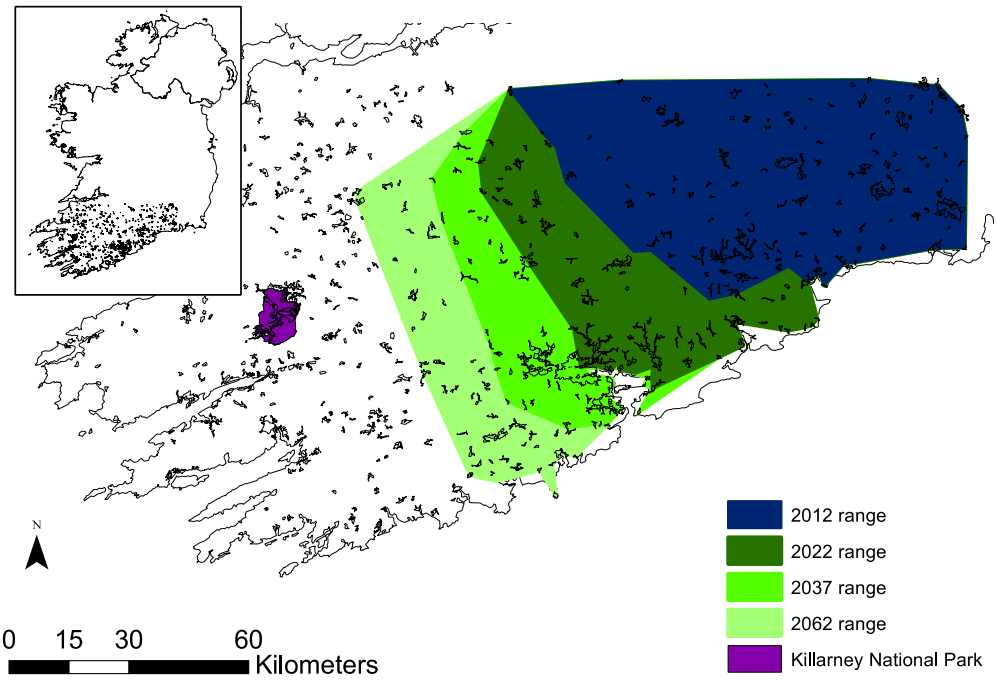
Figure 5.3 Grey squirrel abundances predicted using model 4 (overestimate; red) and model 11 (underestimate; green) during the first 57 years after the introduction and release of 12 grey squirrels (*Sciurus carolinensis*) in Co. Longford in 1911.

5.3.3 Future range expansion and population management strategies

The most valid models, when applied to the still progressing southern range frontier of the grey squirrel in Ireland, predicted continuing range expansion towards the south and west (Figure 5.4) from the current 2012 range. After 25 years, uncontrolled populations were predicted to reach abundances of between 18,416 (± 382) and 19,063 (± 439) grey squirrels occupying 327 – 351 km^2 of suitable habitat patches (Table 5.3) within a minimum convex polygon of 8,039 – 8,923 km^2 in total area. Under these scenarios grey squirrels will reach KNP between 2084 and 2111.



5.4a



5.4b

Figure 5.4 Minimum convex polygons of 2012 grey squirrel (*Sciurus carolinensis*) range and predicted occupancy under no control, 10, 25, and 50 years into the future in the southern region of Ireland using a) model 4 (overestimate) and b) model 11 (underestimate).

Table 5.3a Predicted area of occupied suitable habitat, differences in grey squirrel (*Sciurus* carolinensis) abundance and time to reach Killarney National Park due to management strategies and spatial extents of application 25 years after the latest distribution survey in 2012.

The management strategies are: culls, habitat modification (HM), and immunocontraceptive vaccination (IMC). Model 17 results are displayed in place of model 4 in the IMC scenarios. See Table 5.3b for model 4 results and text for explanation.

Strategy	Control Effort	Spatial Extent	Area by 2037 (km^2)		Abundance by 2037		Year to reach KNP	
			Model 4*	Model 11	Model 4*	Model 11	Model 4*	Model 11
Cull	No Control	-	351	327	19063±439	18416±382	2084	2111
	High	All	317	306	7226±522	7123±532	2111	2124
	High	Buffer	341	319	14823±385	14618±366	2097	2112
	Low	All	347	331	16553±417	16318±400	2087	2103
	Low	Buffer	348	335	17626±424	17303±398	2088	2102
HM	No Control	-	475	464	20228±430	19735±418	2090	2101
	Remove Broadleaf	All	356	249	10144±316	9928±283	2150	2181
	Remove Broadleaf	Buffer	445	427	15498±365	15138±328	2108	2121
	Decrease K	All	335	325	9623±287	9349±255	2105	2126
	Decrease K	Buffer	378	368	15953±386	13845±324	2107	2113
IMC	No Control	-	326	346	12674±274	27603±598	2161	2076
	High	All	318	336	10322±297	25651±453	2186	2079
	High	Buffer	320	344	11467±257	26378±516	2181	2079
	Low	All	324	345	12007±269	26878±528	2169	2078
	Low	Buffer	324	345	12246±271	17203±522	2168	2078

* Model 17 results displayed for IMC scenarios.

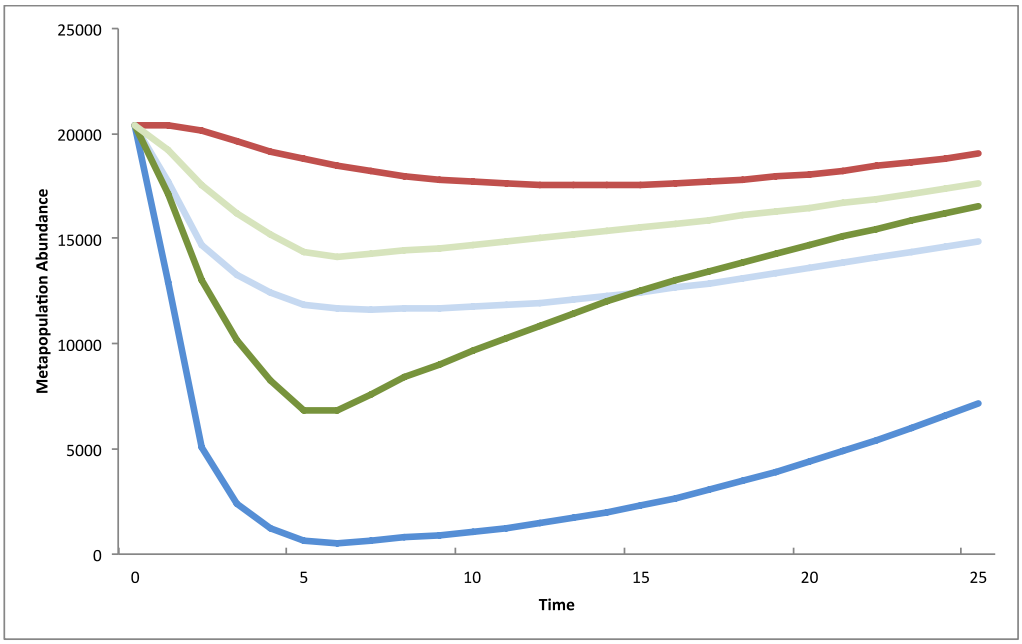
Table 5.3b Predicted area of occupied suitable habitat, differences in squirrel abundance and time to reach Killarney National Park using the parameters of model 4 and immunocontraception management at various levels of effort and spatial extents of application 25 years after the latest distribution survey in 2012.

Strategy	Control Effort	Spatial Extent	Area by 2037 (km^2)*	Abundance by 2037	Year to reach KNP
IMC	No Control	-	150	19±11	-
	High	All	159	48±16	-
	High	Buffer	158	55±17	-
	Low	All	158	53±17	-
	Low	Buffer	159	57±18	-

*maximum area occupied for the complete duration 2012-2037.

High and low effort control strategies carried out both in a focused buffer area and in all patches were compared in order to best guide future management efforts that would minimise cost and effort. A marked decrease in squirrel population abundance is predicted to result when 70% of all yearling and adult squirrels are culled either in the buffer area or in all patches for 5 years, with effects lasting over 20 years from the cessation of the cull programme (Figure 5.5). Model 4 predicted stronger effects of the high intensity cull than model 11 both in overall abundance and time to reach KNP (delaying arrival of the squirrel by 13-27 years in model 4 vs. 1-13 years under model 11 parameters). Effects of the lower effort culls were less apparent two decades after control cessation and showed the undesirable effect of reducing the time to invasion of KNP by 8-9 years in model 11 and only delaying invasion by 3-13 years in model 4.

5.5a



5.5b

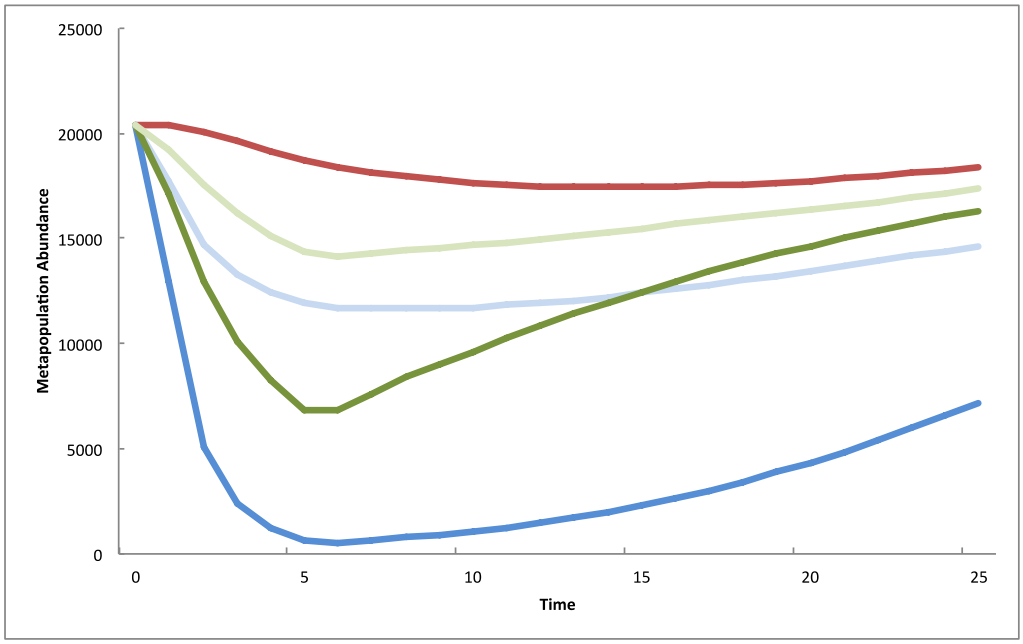
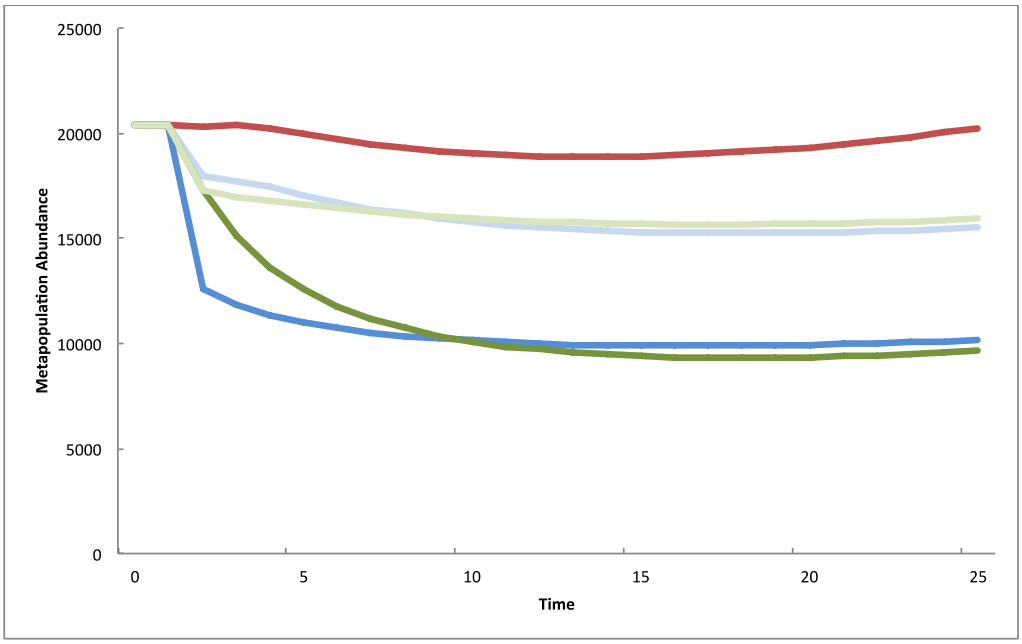


Figure 5.5 Metapopulation abundances for simulated cull control scenarios under a) model 4 and b) model 11 demographic and dispersal parameters. The red line indicates abundance when no culls are applied to the metapopulation. Dark and light blue lines show the grey squirrel abundance predicted to result from a 70% cull on all and buffer populations respectively. Dark and light green lines show the squirrel abundance predicted when culling effort is reduced to 30% of the population for all and buffer populations respectively.

Removing all broadleaf habitat (Figure 5.6) was marginally less effective than decreasing habitat carrying capacity for both models 4 and 11 in reducing overall grey squirrel abundance. When habitat modification was applied in the buffer zones, broadleaf removal outperformed decreasing carrying capacity for squirrel abundance reduction in model 4 but not in model 11. Additionally, the resulting difference in squirrel abundance under model 11 was more pronounced between the two control methods applied in the buffer zone. Habitat modification actions were permanent in the model and therefore abundance recovery was not observed within 25 years of control. Habitat regrowth or regeneration was not considered in the model and would likely have the effect of increasing abundance as habitat regained suitability for grey squirrels. Each of the habitat modification scenarios showed the greatest reduction in occupied area after 25 years from the no control scenario, compared with cull and immunocontraception strategies (Table 5.3a). These habitat based control strategies were also the most effective at extending the time before invasion of KNP. Removing broadleaf at buffer and complete extents extended the time to invasion by 18 and 60 years under model 4 and by 20 and 80 years under model 11. A different pattern held when carrying capacity was reduced, as control applied over the whole region delayed colonisation of the valuable ecosystem by 15 years, but when restricted to the buffer zone it caused a delay of 17 years under model 4.

5.6a



5.6b

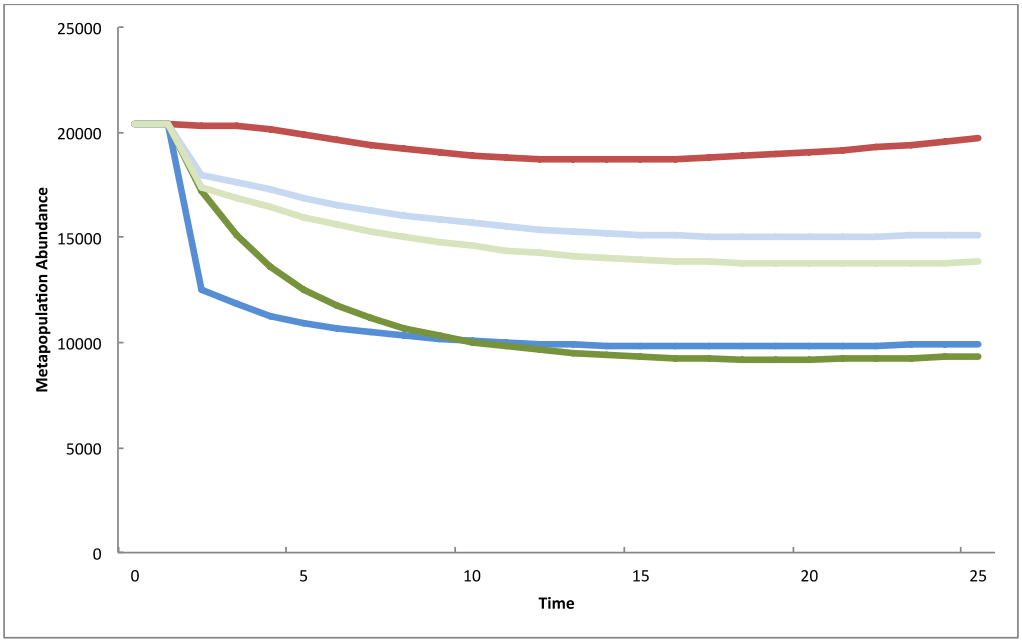
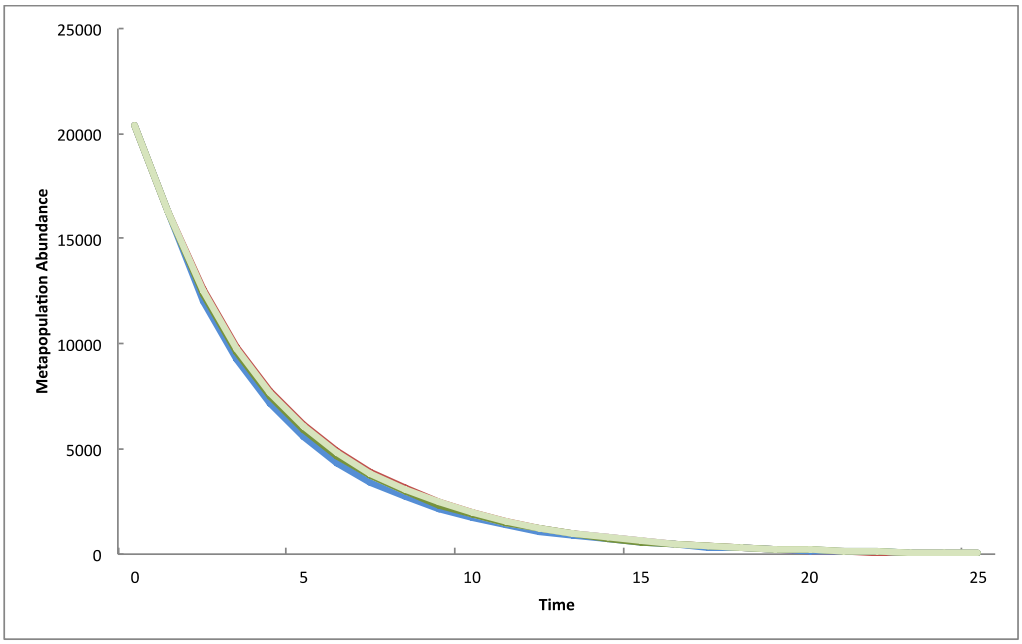


Figure 5.6 Metapopulation abundances for simulated habitat modification control scenarios under a) model 4 and b) model 11 demographic and dispersal parameters. The red line indicates abundance when no habitat modification was performed. Dark and light blue lines show the grey squirrel abundance predicted to result from removing all broadleaf habitat from the entire and buffer regions respectively. Dark and light green lines show the squirrel abundance predicted when the carrying capacity of all and buffer patches was reduced by 50% respectively.

The density dependence function within RAMAS was incompatible with the technique used to modify relative fecundity levels and model the effects of an immunocontraceptive vaccine because it overrides manually adjusted relative fecundity or survival values. In order to allow for the examination of immunocontraception vaccine effects, which was modeled by reducing relative fecundity of populations either by 70% or 30% as described above over the whole or buffer region, it was necessary to modify the density dependence function from the contest function to the ceiling function. Ceiling density dependence is simpler than the contest function, described above, in that under this model the population grows exponentially up to the ceiling (carrying capacity) and then remains at that level until it experiences decline either by random fluctuations or emigration (Akçakaya and Root 2013). The ceiling function does not assume that populations will always recover from low densities as does the contest density dependence function (Akçakaya and Root 2013). After this change was implemented and immunocontraception strategies as well as the "no control" scenario modeled, model 4 predicted the extinction of all grey squirrel populations in the southern region within 50 years of 2012 (Figure 5.7a; Table 5.3b) due to $\lambda<1$ in this model. In order to examine the effects of immunocontraception strategies on a grey squirrel population with the same dispersal parameters as model 4, but with λ just over 1, model 17 was substituted for model 4 in these control scenarios. This model also had a high degree of patch area match between the predicted and observed initial invasion (Table 5.2a) and overestimated occupied area in this region to a slightly greater extent than model 4. The predicted effects of a five-year immunocontraception programme for yearling and adult female squirrels did not last as long as those resulting from culls or habitat modification (Figure 5.7b,c). Vaccinating with 70% effort in all populations for 5 years reduced overall abundance by 7-18% under model 11 and 17 parameters after 20 years, while all other immunocontraception scenarios caused smaller reductions (1-4% for model 11 and 3-9% for model 17). Control of grey squirrel using immunocontraception delayed arrival in KNP of the faster growing model 11 population by 1 to 2 years, and by 8-25 years under model 17.

5.7a



5.7b

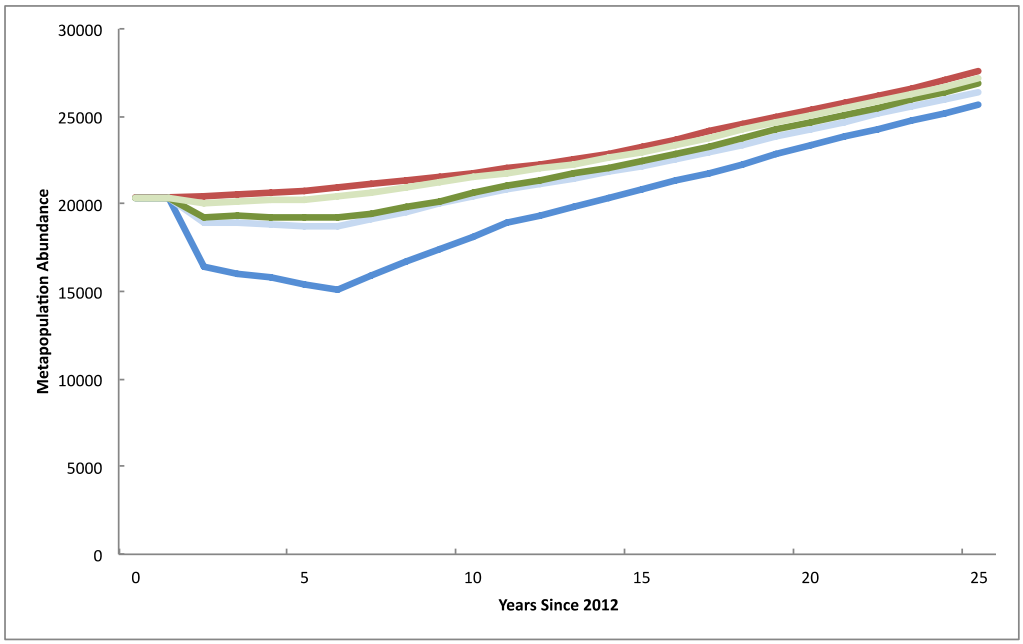


Figure 5.7 Metapopulation abundances for simulated immunocontraception control scenarios under a) model 4, b) model 11 demographic and dispersal parameters. The red line indicates abundance when no vaccination was carried out. Dark and light blue lines show the squirrel abundance predicted to result from vaccinating 70% of all adult and yearling female squirrel from all and buffer populations respectively. Dark and light green lines show the squirrel abundance predicted to result from vaccinating 30% of all adult and yearling female squirrel from all and buffer populations respectively.

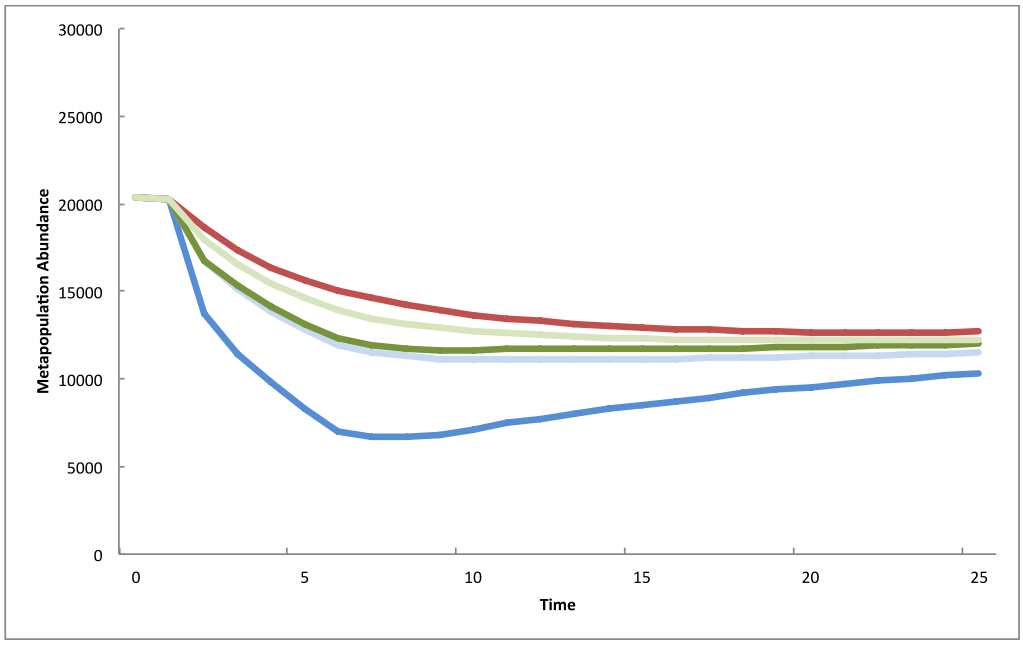
5.7c 

Figure 5.7 cont. Metapopulation abundances for simulated immunocontraception control scenarios under c) model 17 demographic and dispersal parameters. The red line indicates abundance when no vaccination was carried out. Dark and light blue lines show the squirrel abundance predicted to result from vaccinating 70% of all adult and yearling female squirrel from all and buffer populations respectively. Dark and light green lines show the squirrel abundance predicted to result from vaccinating 30% of all adult and yearling female squirrel from all and buffer populations respectively.

5.4 Discussion

The invasive grey squirrel, which has spread through suitable habitat across the island of Ireland, reaching the northern and eastern coasts, continues to expand its range to the south, endangering rare and internationally important woodland ecosystems. A wildlife note published shortly after the 1911 release indicated that the grey squirrel was already considered a pest on estate lands and that control efforts had been unsuccessful in preventing its spread (Watt 1923). Models of squirrel abundance during this initial post-release period show a lag period between introduction and sharp annual increases in abundance, a phenomenon also observed elsewhere in invasive animal populations (Memmott *et al.* 2005; White *et al.* 2012; Bertolino *et al.* 2014). Continued expansion along the southern invasion frontier is predicted in the absence of intensive and prolonged control measures. Long-term

conservation or landscape management of areas within the predicted area of invasion must assess whether grey squirrel presence is incompatible with goals and formulate management strategies and budgets accordingly.

5.4.1 Model assumptions and demographic compensation

Ecological models require the estimation of numerous parameters and for simplifying assumptions about complex natural relationships to be made. Often these assumptions are known to be more or less unrealistic depending on detailed knowledge of the system under consideration, available computer power, and mathematical expertise. As such, it is important to be mindful of these limitations when drawing conclusions and formulating recommendations based on model outputs. Prediction error for the current grey squirrel model was addressed by drawing and/or estimating demographic and dispersal parameters from empirical data from intensively studied populations in both the native and introduced range of this species (Chapter 4; Appendix 3). Systematic variation of these parameters, through the Latin Square format, ensured that the combinations of parameters that led to distributions that best matched the earliest recorded range were retained and used for predictions of future population expansion. The 1968 distribution of grey squirrels in Ireland is known from one source (NPWS 1968) with unspecified survey methodology. Consequently, it is important to recognise that because the population models were calibrated to this distribution, and that current and future population dynamics were assumed to be identical to those in play shortly after the initial introduction, errors in this range will be perpetuated in model results.

The representation of habitat in a SEPM is equally important to the quality of model outputs as are the demographic and dispersal parameters of the focal species. Unfortunately it is easy for the importance of this aspect of model design to be overlooked by ecologists or modelers, whose main focus is at the species level. Map availability is often a limiting factor for the accuracy and precision of input maps. Using 2006 land cover data to model spatially explicit spread in the invading

squirrel during the 1911-1968 time period may have decreased the ability of the current model ability to estimate the true demographic and dispersal dynamics of the introduced grey squirrel population. Indeed, a lack of connectivity between the introduction site and patches in the northern portion of the 1968 distribution prevented this model from predicting initial expansion of squirrels into that area (Figure 5.2). However, the recent programme of afforestation in Ireland that began in the middle of the 20th century mainly supported establishment of conifer plantations on land that was not ideal for other forms of agricultural activities (Hickie 1990). Conifer woodlands were not considered to be suitable grey squirrel habitat in this model and consequently it is unlikely that much of the significant habitat change in the last century would greatly alter the simplified landscape utilised within the model. Limitations on minimum patch and/or population carrying capacity were specified in the model to avoid undue complexity of the patch matrix. Small populations of grey squirrels are undoubtedly important in overall metapopulation functioning and invasion dynamics (Chapter 4). Exclusion of smaller populations ensures that model predictions are conservative rather than overly speculative.

Interestingly, the finite rate of increase of the models that best fit the initial expansion of the grey squirrel in Ireland were composed of survival values much higher than those found in frontier grey squirrel populations (model 4: 52.5%; model 11: 87.5%; model 17: 70%; frontier populations (Chapter 4): 31.7 ± 4.7%). Fecundity was not measured during live trapping fieldwork in Chapter 4 and thus no direct comparison can be made. It is likely though, that fecundity values in the chosen models are higher than researchers would normally expect to find in live trapping and radio-tracking studies given reported values of juvenile survival and breeding rate (Chapter 4; Appendix 3). These disparities highlight that assumptions made during the model design are being compensated for by higher demographic rates. This mismatch between reality and model design is to be expected in population modeling, which as a rule represents a much-simplified version of the natural situation. The simplification of habitat types, consideration of only major grey squirrel populations ($K \geq 50$), as well as the 100 m^2 raster cell size used in patch

identification by the RAMAS spatial data programme could lead to the use of higher demographic rates to recapitulate observed spread over a more conservative simulated landscape. Some of the assumptions related to the yearly time step are difficult to reconcile with species ecology in this system. Particularly problematic is the assumption that no deaths occur between the pre-breeding census and completion of reproduction, a period that may last longer than five months for grey squirrels. It is important to recognise that this compensation is being made and is reflected in the demographic rates used by the models

5.4.2 Comparisons and implications

The grey squirrel population models in this study were designed and analysed following the rationale outlined by Guichón and Doncaster (2008), one of the few examples of SEPM application, so that the design and findings of the two studies could be compared qualitatively in this still evolving field. Though the focal species and habitats are different, comparison of squirrel invasion SEPMs should highlight important trends or avenues for future research. The inclusion of density dependent dispersal in the model design reduced predicted spread into suitable habitat patches. This increased the match between predicted and observed occupied habitat for the red-bellied squirrel invasion (Guichón and Doncaster 2008) but generally decreased the match for the Irish grey squirrel invasion (Table 5.2). It is possible that this phenomenon is due to the shorter period over which the initial invasion was considered in Argentina (31 years) compared with the Irish invasion model (57 years). Empirical determination of the influence of density dependent effects on squirrel populations and how these change with time since invasion could improve future population models with the incorporation of such information (using a user-defined function) into RAMAS models. Large-scale culls have been repeatedly identified in SEPM models as the most effective method of invasive squirrel control (Rushton *et al.* 2002; Bertolino *et al.* 2008; Guichón and Doncaster 2008) and intensive culls were again found to be the most effective abundance reduction method in the current study. Habitat modification through carrying capacity

reduction was rejected as a viable management option in Argentina, after unfavourable acceleration of expansion was predicted (Guichón and Doncaster 2008). Similar scenarios in Ireland, however, did not predict the same undesirable result from this management method. More detailed models, at finer scales, may clarify the appropriateness of this type of habitat modification for invasive squirrel control. Previously, a bespoke SEPM (Rushton *et al.* 2002) showed that a hypothetical immunocontraceptive vaccine (of a different type than that modeled here) was not effective at reducing effects of grey squirrel invasion, unless applied at large scale. Immunocontraception programmes in the current model showed limited effectiveness in reducing regional abundance and expansion at all scales and intensities. Agreement between these two models strengthens the assertion that immunocontraception, though a valuable control method, is best suited to certain limited situations or as part of an integrated control strategy. More localised modeling of specific immunocontraception strategies could assist in the design of such programmes.

The predicted outcomes of the various control scenarios should be considered cautiously because, like the demographic and dispersal processes, the cull and immunocontraception control actions took place discretely, once per time step, in the model. Lawton and Rochford (2007) found that local population culls suppressed grey squirrel abundances for just a few months before dispersal from nearby populations or surrounding suboptimal habitat filled vacant habitat. It is likely that longer lasting results could be achieved if control was applied to all populations in an area in a coordinated manner to reduce opportunistic dispersal outside of seasonal movement. Successful invasive species eradication and long-term control has rarely if ever been achieved in Europe, where the high costs for requisite equipment and labour, as well as ethical resistance to fatal measures (Bertolino and Genovesi 2003; Bremner and Park 2007), has hampered efforts (but see Gosling and Baker (1989); Tonkin and Mackenzie (2011)). Predictive models, such as those considered here, can guide conservation managers and government organisations toward the most effective strategies by allowing for the avoidance of

expensive and potentially unproductive experiments in control methodology and for the speedy implementation of effective management measures.

5.4.3 Control strategies

Species population models are valuable tools that can assist scientists and conservation managers in making informed management decisions where experimental testing of alternative management strategies is difficult or costly. It was possible, in this way, to evaluate predicted outcomes of alternative grey squirrel control strategies with a far smaller investment of time and resources through the simulation of expanding populations and control measures. The traditional method of controlling grey squirrels is through culling animals by trapping or shooting (Bertolino and Genovesi 2003; Lawton and Rochford 2007). Results of the model indicate that 5-year intensive, coordinated region-wide culls (≥ 70% of adult squirrels culled in all significant populations) would be successful in sharply reducing squirrel numbers in the short and medium term (at least 20 years post management action cessation). However, the metapopulation was predicted to increase in abundance and range extent (i.e. reach Killarney National Park more quickly) at a faster rate after the cessation of low intensity culls, suggesting that unfavourable density dependent consequences of squirrel removal could occur at low levels of fatal control. These results further support assertions that successful control measures should be nationally managed (Mack *et al.* 2000; Bertolino and Genovesi 2003) and that sporadic, uncoordinated, or low intensity level culling may in fact cause faster population abundance or range increases. Promisingly, a strategically coordinated grey squirrel culling programme in Aberdeenshire, Scotland has succeeded in reducing grey squirrel abundance and halting range expansion (Tonkin and Mackenzie 2011). The control project, which benefited from multiple funders and stakeholders, was based on long-term research into grey squirrel populations in the area and was well situated to manage culling effort adaptively as monitoring continued simultaneously. Lessons learned during the

Scottish cull could be adapted to prevent or slow grey squirrel expansion in the south of Ireland or elsewhere where grey squirrels are predicted to invade.

Habitat modification via the removal of broadleaf habitat was not predicted to lower grey squirrel abundance as much as intensive culls but the effect persisted over the short and medium term and was predicted to delay the arrival of grey squirrels at KNP by between 18 and 80 years depending on the spatial extent of modification. Though promising results were predicted from these actions, the likelihood of negative ecosystem-wide effects should be carefully considered before the implementation of such radical methods over a wide area. Rare Irish broadleaved woodland habitats, which support unique ground flora and fauna, are of high conservation value and consequently planting and protection is actively encouraged (Poole *et al.* 2003). Removal of broadleaf habitat from a buffer area also severely decreased connectivity of habitat patches for the grey squirrels and effectively delayed range expansion. Careful assessment and more focused modeling could identify areas within the southern region of Ireland in which the ecological and financial costs of habitat removal or land use change could be outweighed by a reduced or delayed risk of grey squirrel invasion. Decreasing patch carrying capacity as suggested by Guichón and Doncaster (2008) for squirrel control could be achieved through the restriction of accessibility (e.g. exclusion devices on tree trunks) and suitability (tree species replacement, nest removal) of all habitat types to squirrels. Though this control method also showed promising results, it is likely that costs of material and labour as well as negative ecological impacts on other species would rule out extensive implementation of this strategy in Ireland.

Though an immunocontraceptive vaccination programme succeeded in preventing reproduction in a fox squirrel (*S. niger*) population (Krause *et al.* 2014) and the technique showed promise in a small trial involving grey squirrels (Pai *et al.* 2011), the capacity of a large scale vaccination programme to control invading squirrel populations is unknown. Here, results indicate that an intensive 5-year vaccination programme performed region-wide (70% of yearling and adult females treated in all populations) would cause a short-term reduction in population abundance but that

medium term effects would be negligible. Immunocontraception programmes were predicted to cause a smaller delay in the invasion of KNP by grey squirrels under the high λ model (model 11) than under a model with λ just marginally larger than 1 (model 17). Vaccination programmes carried out over the strategic buffer populations only, or at a lower intensity, were not effective at decreasing abundance and bring further support to large coordinated control campaigns over local or low-intensity efforts. The nature of this control method, which would require more extensive training for control staff and material expense than culling programmes, makes it unlikely that anything other than local applications of control could feasibly take place. Compensatory mechanisms acting to boost survival of juveniles (Jacob *et al.* 2004) or fecundity of untreated females could diminish population size reductions, achieved through control programmes, if less than 100% of breeding females are treated. Fertility reduction techniques alone were not shown to be sufficient to effectively control invading grey squirrel populations. However, such techniques could improve management outcomes if used to complement more effective strategies such as culling in areas where fatal control is inappropriate or unwanted (e.g. suburban areas) (Lauber and Knuth 2004).

Invasion frontier-based control programmes offer a less expensive alternative to region-wide strategies. However, when these scenarios were considered for the grey squirrel invasion in Ireland, under the buffer scenarios, the effects were not consistently comparable to region-wide action. In the case of fatal control options, frontier-based efforts were much less effective than region-wide programmes in slowing expansion. This contrasts with results found in Argentina, where the difference in expansion after priority culls and region-wide culls was much smaller for red-bellied squirrels (Guichón and Doncaster 2008). Interestingly, decreasing carrying capacity in the frontier area habitat for model 4 caused range expansion to be slightly slower than did the region-wide application of similar control. It is possible that, when examined from a cost-effectiveness point of view, the savings in cost associated with a more limited control region may outweigh the decrease in effectiveness of control.

5.4.4 Synthesis

Grey squirrel range is predicted to continue to expand in the absence of effective coordinated control programmes in the south of Ireland. Minimum convex polygons, the standard method utilised to estimate species range boundaries, are prone to overestimate range or to be insensitive to changes in occupancy inside vertices at the extremes (Burgman and Fox 2003). The polygons used in the current study to describe predicted uncontrolled grey squirrel expansion, though modified to respect coastlines, likely mask effects of habitat and connectivity on the invasion frontier. The frontier may progress more quickly in areas of high connectivity but low carrying capacity, as dispersers must travel greater distances to find adequate home ranges, than in resource-rich or sparsely occupied areas where suitable unoccupied habitat exists nearby. Events not considered in the simulations, such as human-mediated long-distance movement events, complete long-lasting seed crop failure, or predator population dynamics (Sheehy and Lawton 2014) could significantly alter future grey squirrel invasion dynamics. Remaining mindful of such sources of error, predictions of future grey squirrel range expansion are valuable to diverse interest groups. Conservation managers focusing on red squirrel protection can use these estimates to plan reserve areas or to begin the lengthy process of acquiring funding for local control or defense projects before it is urgently needed. Alternatively, silviculturists and landowners can avoid planting tree crops prone to bark stripping damage within the predicted range, or plan crops so that they are in a less vulnerable age class when squirrels reach the area. In essence, these predictions set the stage for proactive rather than reactive grey squirrel management in the south of Ireland.

Predictions generated by SEPMs are testable and models should continually be enhanced and modified as more accurate or tailored demographic and habitat data become available. An honest understanding of the assumptions made during the model design process can guide empirical work aimed at removing those assumptions or reducing their simplifying effects. In the case of the invasive grey

squirrel in Ireland models predict persistent south and southwest range expansion unless effective, coordinated, and regular control efforts can be implemented. These investigations have exposed the potential implications of such measures. A formal cost-benefit analysis and a public opinion education campaign regarding control methodologies (Bremner and Park 2007) should be the next step to objectively evaluate control regimes.

Chapter 6 –

Conclusion

A grey squirrel in a trap in Cahir Park, Co. Tipperary, Ireland

6.1 Informed predictions rely on accurate location and demographic data

To effectively safeguard vulnerable species and ecosystems in a rapidly changing world, it is necessary to gain a more complete understanding of the processes that influence further spread of established biological invasions, one of the leading causes of world-wide biodiversity decline (Vitousek *et al.* 1997; McGeoch *et al.* 2010). This thesis aimed to provide an improved understanding of the particular importance of invasion frontiers, and the populations thereon, to the dynamics of species invasions. This was achieved through a multi-pronged and sequential approach centered on investigating the currently expanding southern frontier of the invasive grey squirrel in Ireland. Although each data chapter is presented as a discrete entity in this thesis, they provide a fuller picture of grey squirrel frontier population functioning together than they do separately. A synthesis focusing on the intertwining themes and findings of these data is therefore worthwhile.

The natural starting point for this project was the identification of the current southern grey squirrel frontier, accomplished in chapter 2. The differences in the cost-effectiveness, efficiency, and abilities of the citizen science survey and the traditional hair-tube survey were substantial. Survey methods involving the public have shown great promise in fulfilling diverse aims such as species monitoring (Eraud *et al.* 2007; Peacock *et al.* 2007) and disease tracking (Koenig *et al.* 2007; LaDeau *et al.* 2007) as well as public engagement and education (Delaney *et al.* 2008; Braschler 2009). The citizen science survey returned a more up-to-date and cost-effective snapshot of the location of the invasion frontier over a much larger geographic region than the hair-tube survey. Furthermore, the majority of the benefit of the citizen science survey, in terms of sighting locations and the basic outline of the invasion frontier, was realised in the first 6 – 12 months of the survey. Had the survey been wound up at that point the differences in overall cost-effectiveness and efficiency between the two methods likely would have been greater. The results of this chapter also challenged the previously-held notion that hair tubes are well-suited for detecting colonising populations of grey squirrels (Finnegan *et al.* 2007). The hair-tube survey did, however, identify four sites (not including two additional sites

in which grey squirrels were observed during fieldwork) of appropriate size (minimum 30 ha) that supported grey squirrel populations close to the frontier. Two of these sites, Cahir Park and Kilnamack Wood, were chosen for further behavioural and demographic investigation by live trapping.

The 22-month live trapping study formed the basis of the next three chapters. Originally it was envisioned and designed as a purely demographic investigation but the behavioural element was added in the spring of the first trapping year. The functional behaviour and personality of individual members of a population, as well as inter-population differences in these traits, have been linked to invasion and range expansion processes (Rehage and Sih 2004; Duckworth and Badyaev 2007; Cote *et al.* 2010b; Fogarty *et al.* 2011; Chapple *et al.* 2012). These studies have found that invaders or members of frontier populations tend to be more aggressive and/or bolder and that the inclusion of a personality component can improve models predicting invasion success. In the current study, baseline personality measures were collected from frontier grey squirrel populations using simplified and inexpensive data-collection techniques. Although sciurids are a common study species in personality research (e.g. Boon *et al*. (2007); Boyer *et al*. (2010); Patterson and Schulte-Hostedde (2011)), the grey squirrel specifically has, to-date, not featured largely in this field (but see Pasitschniack-Arts and Bendell (1990)). This study identified that personality in this species is influenced by state and individual-based variation. The groundwork is now laid in this species system for future work designed to examine how grey squirrel personality across populations might vary with *inter alia* time since invasion.

The demographic and biological data gained on the two frontier populations over the course of the live trapping study filled a gap in Irish squirrel research, all of which had previously collected data from introduced grey squirrel populations in established areas of the range (O'Teangana 1999; Lawton and Rochford 2007; McGoldrick 2011; Sheehy and Lawton 2014). Similarly, outside of Ireland few studies have collected demographic data from frontier populations (but see Wauters *et al.* (2000); Gurnell *et al.* (2001)), although the species is very well studied across

the native and introduced ranges. Through comparison, it was found that differential reported impacts of the invading squirrel in different countries are reflected in the demographic rates (i.e. density, survival and breeding rate) observed across these areas. Furthermore, the results of the comparison highlighted that frontier introduced populations are at lower density than established or native populations and display signs of increase, rather than maintenance, through higher survival and breeding rates. It is known from the citizen science survey in chapter 2 that the frontier populations trapped in the current study were not on the leading edge of grey squirrel range expansion when trapping took place. Indeed, members of the public provided information that grey squirrels had been present in the sites for a number of years before the trapping programme was initiated (Cahir Park: 10 years; Kilnamack Wood: 2 years). That the demographic rates recorded from these two sites generally align with those found from other frontier areas confirms that these populations are indeed correctly categorised as "frontier". It is clear from these results that population increase to carrying capacity and demographic normalisation (e.g. a stable age distribution or settlement of available home ranges) occurs over multiple squirrel generations and that range expansion continues to progress while this process is happening (in contrast to expansion taking place only after frontier populations reach carrying capacity and extra-population dispersal is forced). This finding along with previous work on personality in expanding populations of other species, which showed that individuals on the frontier are more prone to dispersal and possess more aggressive or bold personalities (Rehage and Sih 2004; Duckworth and Badyaev 2007), suggest that this species system may also demonstrate these personality trends and that further investigation is warranted.

Realistic and evidence-based grey squirrel population modeling would not have been possible without the demographic comparisons made in chapter 4. The collation of previously collected data allowed for estimation of survival and fecundity parameters that were based in fact. Although model assumptions eventually resulted in higher than expected demographic rates being retained in the final models, this fact does not negate the effort invested in choosing the most realistic and defensible values possible. Model outputs, namely future uncontrolled

range expansion, provided testable predictions. These predictions can inform the initial design stages of future frontier surveying or trapping studies by identifying areas predicted to be occupied each year into the future. The results of future distribution surveys, perhaps utilising citizen science methodologies, can be compared to the model range predictions. These comparisons can inform and improve the choice and design of future models as well as the accuracy of range expansion predictions. The evaluation of the effects of hypothetical control strategies at different intensities and scales within the model provided further support for previous recommendations and highlighted predicted differences in management method effectiveness. Many authors have argued that successful management or eradication of invasive species requires the commitment of the public, scientific community, and governing bodies to well-supported and coordinated control efforts (Mack *et al.* 2000; Bertolino and Genovesi 2003; Guichón and Doncaster 2008; Bryce *et al.* 2011). Results from the current study support these recommendations and predict that region-wide application of intensive control methods, particularly culls, would achieve the strongest result in terms of reduction in abundance and occupied area. Based on model results, caution is advised against investment in and broad-scale application of immunocontraceptive methods that are currently under development. These strategies were not predicted by the model to cause an appreciable management result, at the regional scale, despite promising individual population-level effects having been found experimentally (Krause *et al.* 2014).

6.2 Evaluation of methods and future research opportunities

6.2.1 Citizen science survey design

The simplicity and straightforwardness of the citizen science survey project to detect squirrel presence was one of its greatest strengths. However, when it came to analysis of the data collected, it became apparent that more and better quality information could have been collected from the public with small survey design modifications. It is recommended that questionnaires and other public surveys be

pilot-tested to identify issues (White *et al.* 2005) and, if time had allowed, this undoubtedly would have allowed for improvement of the survey. It would have been particularly interesting to examine the difference in habitat types of sighting locations, following survey improvement, as discussed in chapter 2. These changes would have made the survey form slightly more complex for the volunteer to complete so the gain in data quality may have been accompanied by a small cost in volunteers becoming overwhelmed and not bothering to submit sighting reports.

Future squirrel surveys in Ireland could benefit from the creation of a free smartphone application with GPS recording capabilities. Application development costs are becoming more reasonable and to save funds, if the survey project is university based, collaboration could be sought with the computer science department or their students. An example of this type of data collection method in practice is "Project Squirrel" (http://www.projectsquirrel.org/) based in Chicago, Illinois and administrated by a partnership between the Peggy Notebeart Nature Museum and the University of Illinois at Chicago. In 2013, 57% of those aged 18 and older used a smartphone in Ireland (Anon. 2014) demonstrating that such survey methods are appropriate in this market. An application with social-media sharing capabilities would also serve to generate more publicity for the survey and ultimately more responses.

6.2.2 Detection probability

The hair-tube survey methodology followed in chapter 2 is well-established and used internationally (e.g. Gurnell *et al*. (2004a); Finnegan *et al*. (2007); Bertolino *et al*. (2009)). A weakness in the application of single 14-day surveys in each site for species presence was that the detection probability of grey squirrels using this method was unknown. Detection probability (p) is the probability that a present species will be detected. The value can be numerically estimated after repeated sampling sessions using Program PRESENCE (http://www.mbr-pwrc.usgs.gov/software/presence.html) which resembles Program MARK used in

chapter 4 to estimate survival and recapture probabilities. In Program PRESENCE, Ψ denotes probability of site occupancy and p represents detection probability, similar to ϕ (probability of survival) and p (recapture probability) in Program MARK. Repeated sampling sessions, required to calculate detection probability, did not have a place in the comparison between the citizen science and hair-tube methods. Detection probability for grey squirrels using hair tubes in Irish habitat types should be calculated and could be carried out in a manner similar to work already published on red squirrels in Italy (Mortelliti and Boitani 2008; Mortelliti *et al.* 2010; Amori *et al.* 2012). It would be worthwhile to investigate how habitat, time of year, presence of red squirrels, and proximity to the invasion frontier influence hair tube detection probability in grey squirrels.

6.2.3 Personality

One of the more interesting facets of research into animal personality is in examining how variation in personality influences, or alternatively is influenced by, variation in life history strategies or reproductive success. In the current study the NSW (nipples swollen) female breeding condition was assumed to represent successful reproduction. A similar assumption could not be made for male squirrels as their state of testicular development does not indicate mating success, rather it displays capability. If additional resources (e.g. funding, time, training) had been available, it would have been possible to gain better measures of reproductive success either through radio-tracking NSW females to their nests and marking the pups as in Boon *et al*. (2007) or through genotyping adult and juvenile squirrels to gain data on maternity and paternity, similar to Patterson and Schulte-Hostedde (2011).

There is much more knowledge to be gained through further investigation into grey squirrel personality. It would be particularly interesting to record results comparable to the current study from populations with different times since colonisation. This type of study would be a large undertaking and require site replication for each

distance from the frontier (as a proxy for time since colonisation). Habitat type, human site use, and red squirrel presence in the site should also be carefully considered in the study design. With the appropriate choice of sites, each of these variables could be examined for their influence on expression of grey squirrel personality.

6.2.4 Invasion frontier demography

The categories and quantities of information gained on mammal populations from long-term live trapping studies are unmatched by any other less intensive survey method. Unfortunately, the very scale and expense in equipment and time required for these studies can lead to a level of "scientific inertia" in the deployment and establishment of successful trapping field sites. Many of the peer-reviewed live trapping studies on red and grey squirrels in Europe examined and/or compared aspects of one or two populations (e.g. Lurz *et al*. (2000); Gurnell *et al*. (2001); Bryce *et al.* (2002); Wauters *et al.* (2004); Lawton and Rochford (2007)) though research teams have been able to compare greater numbers of populations (Kenward *et al.* 1998; Gurnell *et al.* 2004b). Given a research or fieldwork team and significantly more funding and resources than are generally available for a PhD project, a large scale trapping programme that is both adaptive and long-term could be designed to carefully record the multi-year processes that occur as a site is colonised by grey squirrels and they become established. Site selection could be adaptive and staggered in that trapping programmes could be instituted as soon as new grey squirrel populations are identified. Trapping in each site would then continue for a number of years until rapid population growth ceases and carrying capacity is approached. Enough trapping sites could be chosen to ensure replication of site characteristics. A research programme of this ambitious scale is, unfortunately, unlikely to secure sufficient funding. Projects that are successfully funded are often able to address key management questions in a cost-effective manner. The project described above, though potentially able to provide fascinating

insight into invasion frontier and colonisation processes, would essentially expand on research and management questions already addressed in this thesis.

The demographic comparison of native and introduced grey squirrel populations highlighted specific combinations of site characteristics (habitat, colonisation status, country) that are under- or unrepresented in the body of scientific literature. Benefit would be gained from filling these gaps with new live trapping studies. With sufficient data, statistical investigations would strengthen or adapt the trends in demographic rates qualitatively identified in chapter 4. Ideally a meta-analysis of grey squirrel demography could be performed. The difficulties involved in conducting such analyses on ecological data remain significant, and are often due to missing data values and differences in methodology between studies, as found by Koprowski (2005).

6.2.5 Population modeling

The major criticism of population models, indeed all models, is that the assumptions and simplifications made during the design process lead to outputs that do not directly reflect the real world situation. Statistician George E. P. Box elegantly sums up this criticism in the quote "essentially, all models are wrong, but some are useful." At this point, the usefulness of models in ecology is well understood and accepted by the field. As long as assumptions and limitations are clearly stated, the contributions of models to the fields of ecological research and applied management are invaluable.

A natural progression from the grey squirrel modeling work in chapter 5 would be a cost-effectiveness analysis of different control strategies. Such a comparison would require the design and costing of hypothetical control programmes. It would be difficult to estimate cost details for immunocontraceptive vaccines as further improvements are required in the conjugate or preparation before they can become commercially available for use in squirrels (Krause *et al.* 2014). Conveniently, the

capability exists within RAMAS GIS 6.0 to compare costs and benefits of multiple population viability analyses (Akçakaya and Root 2013) and this function should be utilised for any cost-effectiveness analysis.

The recent resurgence of pine marten populations in Ireland is correlated with localised grey squirrel decline and red squirrel recolonisation (Sheehy and Lawton 2014). Although RAMAS models single-species systems, the potential effects of pine marten presence could be simulated by altering survival and/or fecundity rates in the Leslie matrix for certain populations. The RAMAS user manual states that those with advanced programming and modeling experience could create a separate programme linked with RAMAS GIS via a user-defined function to facilitate simultaneous modeling of multiple species (Akçakaya and Root 2013). The importance of customizable model design systems, such as RAMAS or VORTEX, centers on the fact that they can be quickly and creatively adapted to examine multiple facets of a species system.

6.3 Recommendations and implications for future management

6.3.1 Species distribution surveys

The implications of the current research for future grey squirrel and invasive species management in Ireland are significant. Firstly, the success of the citizen science survey has proven the utility of this method in Ireland for tracking invasive species range expansion. Continued monitoring of the grey squirrel range in Ireland is critical. Recent work has also confirmed that the Irish public is capable of recording grey squirrel range contraction, possibly caused by a resurgence in a native predator, the pine marten (*Martes martes*) (Sheehy and Lawton 2014). Currently, squirrel species distribution records are updated in Ireland regularly (O'Teangana *et al.* 2000a; Carey *et al.* 2007), a trend that will hopefully continue into the future. The 2012 distribution report (Lawton *et al. In prep.*), will be based in part on work carried out for chapter 2. Regulatory bodies can base management recommendations on the results of this and other publicly collected datasets. Lessons learned from the

design, maintenance and analysis of the citizen science survey in the current project can be used to improve the quality and cost-effectiveness of future squirrel surveys in Ireland and elsewhere in the introduced range. Furthermore, monitoring programmes focused on other readily observable and identifiable species, either vulnerable or invasive, in Ireland and elsewhere could be improved or enhanced by adopting recommendations resulting from the work in chapter 2 and the further recommendations above.

6.3.2 Prediction-based management goals

In an ideal situation, invasive species would be removed and controlled shortly after identification, while populations are still small and localised. Unfortunately, this has rarely happened for grey squirrels and eradication of this species is now unrealistic in all European countries where it is present. The most successful grey squirrel management programme to-date centers around the prevention of northward expansion by grey squirrels in Scotland (Tonkin and Mackenzie 2011) although recent pine marten range expansion and recolonisation (Croose *et al.* 2013) may actually be responsible for some of that success in light of correlations recently found in Ireland (Sheehy and Lawton 2014). The well-funded Scottish project oversaw three types of culls: 1) culls performed by project staff, 2) culls under 5-year contracts with estates, and 3) a trap loan scheme to estates and individuals. Although important data were also generated, if the 2-year cost-effectiveness statistics (2009-2011) were analysed for the first cull type alone then cost per squirrel culled was £84.55 (Tonkin and Mackenzie 2011). That cost is significant and such spending, if publicly funded, must be justified with results. It is unlikely that funding of this magnitude will be available in Ireland, in the near future, due to economic conditions and spending priorities. Though the initiation of properly supported region-wide control is doubtful in the near term, predictive models of the kind designed in this study could be used to inform more localised efforts. Modeling the effects of proposed control programmes should highlight possible problems or

unforeseen negative effects, such as rapid population recovery seen after low intensity culls in chapter 5.

Given the unlikely event of successful and permanent local grey squirrel removal or invasion prevention, it is important that focus also be turned to techniques designed to ameliorate the negative effects caused by grey squirrel presence. The major negative impacts experienced as a result of grey squirrel presence are native red squirrel decline and forestry crop damage. Conservation projects have already successfully introduced red squirrels to the west of Ireland into habitats unlikely to experience invasion by grey squirrels in the near future (Poole and Lawton 2009; Waters and Lawton 2011). Food stations that exclude grey squirrels are also useful in providing red squirrels extra resources in the face of competition from grey squirrels (Pepper 1993). Recommendations for forestry crop management and short term strategic culling programmes have shown promise for reducing overall bark stripping impact where applied (Lawton 2003; Lawton and Rochford 2007). Cost-effectiveness analysis of these techniques and potential strategies for their application could identify areas where the most benefit, either for red squirrel conservation or forestry protection, could be gained for the least cost. The current extent of invaded range and predictions for future grey squirrel range expansion discussed in this thesis can guide these investigations and management plans.

6.4 Conclusion

This thesis provides and discusses novel data relating to the current location, behaviour, demography, future expansion and potential management of grey squirrel populations at the southern frontier of the invasion in Ireland. Implications for future applied species management and research are identified and briefly considered. This research considerably benefited from the many important contributions of scientists that had previously studied grey and other squirrel species all over the world. The grey squirrel is the most commonly introduced and established invasive squirrel species (Bertolino 2009) and its continued presence outside of its native range is

assured. Realistic and justified ongoing management of, and research into, aspects of these irreversible invasions will bring further knowledge and expertise that can be usefully adapted to other biological invasions. Therefore, although the local ecological and economic impacts of grey squirrel invasions are commonly negatively viewed, invasion ecology stands to benefit from the careful study of these invasion events.

7.0 – References

Akçakaya HR (2000) Population viability analyses with demographically and spatially structured models. *Ecological Bulletins* **48**, 23-38.

Akçakaya HR, Root WT (2013) RAMAS GIS: linking spatial data with population viability analysis (version 6.0). In. ' (Applied Biomathematics: Setauket, New York)

Amori G, Mortelliti A, Guidarelli G, Schiavano A, Luiselli L (2012) Detectability of the European red squirrel (*Sciurus vulgaris*) in a Mediterranean area. *Rendiconti Lincei* **23**(2), 203-206.

Anderson DR, Burnham KP (1999a) General strategies for the analysis of ringing data. *Bird Study* **46**(S1), S261-S270.

Anderson DR, Burnham KP (1999b) Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study* **46**(S1), S14-S21.

Anon. (2007) National forest inventory Republic of Ireland results. Forest Service, Johnstown, Wexford.

Anon. (2014) 'Our mobile planet - smartphone penetration.' ThinkInsight with Google Available at: http://think.withgoogle.com/mobileplanet/en/graph/?country=ie&category=DETAILS&topic=Q00&stat=Q00_1&wave=2013&age=all&gender=all&chart_type=&active=country Accessed: 28th April 2014.

Aquiloni L, Martín MP, Gherardi F, Diéguez-Uribeondo J (2011) The North American crayfish *Procambarus clarkii* is the carrier of the oomycete *Aphanomyces astaci* in Italy. *Biological Invasions* **13**(2), 359-367.

Ariyomo TO, Watt PJ (2012) The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Animal Behaviour* **83**(1), 41-46.

Barea-Azcón JM, Virgós E, Ballesteros-Duperón E, Moleón M, Chirosa M (2007) Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. *Biodiversity and Conservation* **16**(4), 1213-1230.

Barkalow Jr FS, Hamilton RB, Soots Jr RF (1970) The vital statistics of an unexploited gray squirrel population. *The Journal of Wildlife Management* **34**(3), 489-500.

Benitez VV, Almada Chavez S, Gozzi AC, Messetta ML, Guichon ML (2013) Invasion status of Asiatic red-bellied squirrels in Argentina. *Mammalian Biology - Zeitschrift für Säugetierkunde* **78**(3), 164-170.

Bertolino S (2009) Animal trade and non-indigenous species introduction: the world-wide spread of squirrels. *Diversity and Distributions* **15**(4), 701-708.

Bertolino S, Genovesi P (2003) Spread and attempted eradication of the grey squirrel (*Sciurus carolinensis*) in Italy, and consequences for the red squirrel (*Sciurus vulgaris*) in Eurasia. *Biological Conservation* **109**(3), 351-358.

Bertolino S, Lurz PWW (2013) Callosciurus squirrels: worldwide introductions, ecological impacts and recommendations to prevent the establishment of new invasive populations. *Mammal Review* **43**(1), 22-33.

Bertolino S, Lurz PWW, Sanderson R, Rushton SP (2008) Predicting the spread of the American grey squirrel (*Sciurus carolinensis*) in Europe: A call for a co-ordinated European approach. *Biological Conservation* **141**(10), 2564-2575.

Bertolino S, Montezemolo NC, Preatoni DG, Wauters LA, Martinoli A (2014) A grey future for Europe: *Sciurus carolinensis* is replacing native red squirrels in Italy. *Biological Invasions* **16**(1), 53-62.

Bertolino S, Wauters L, Pizzul A, Molinari A, Lurz P, Tosi G (2009) A general approach of using hair-tubes to monitor the European red squirrel: a method applicable at regional and national scales. *Mammalian Biology* **74**, 210-219.

Betini GS, Norris DR (2012) The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Animal Behaviour* **83**(1), 137-143.

Bled F, Royle JA, Cam E (2011) Hierarchical modeling of an invasive spread: the Eurasian collared-dove *Streptopelia decaocto* in the United States. *Ecological Applications* **21**(1), 290-302.

Bolger DT, Morrison TA, Vance B, Lee D, Farid H (2012) A computer-assisted system for photographic mark–recapture analysis. *Methods in Ecology and Evolution* **3**(5), 813-822.

Boon AK, Réale D, Boutin S (2007) The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters* **10**(11), 1094-1104.

Boon AK, Réale D, Boutin S (2008) Personality, habitat use, and their consequences for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* **117**(9), 1321-1328.

Bosson CO, Islam Z, Boonstra R (2012) The impact of live trapping and trap model on the stress profiles of North American red squirrels. *Journal of Zoology* **288**(3), 159-169.

Bosson CO, Palme R, Boonstra R (2013) Assessing the impact of live-capture, confinement, and translocation on stress and fate in eastern gray squirrels. *Journal of Mammalogy* **94**(6), 1401-1411.

Boudouresque CF, Verlaque M (2002) Biological pollution in the Mediterranean Sea: invasive versus introduced macrophytes. *Marine Pollution Bulletin* **44**(1), 32-38.

Bouffard SH, Hein D (1978) Census methods for eastern gray squirrels. *The Journal of Wildlife Management* **42**(3), 550-557.

Bowers MA, Breland B (1996) Foraging of gray squirrels on an urban-rural gradient: use of the Gud to assess anthropogenic impact. *Ecological Applications* **6**(4), 1135-1142.

Boyer N, Réale D, Marmet J, Pisanu B, Chapuis JL (2010) Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology* **79**(3), 538-547.

Braschler B (2009) Successfully implementing a citizen-scientist approach to insect monitoring in a resource-poor country. *BioScience* **59**(2), 103-104.

Bremner A, Park K (2007) Public attitudes to the management of invasive non-native species in Scotland. *Biological Conservation* **139**(3,4), 306-314.

Bremner-Harrison S, Prodohl PA, Elwood RW (2004) Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Animal Conservation* **7**(3), 313-320.

Brown BW, Batzli GO (1985) Field manipulations of fox and gray squirrel populations: how important is interspecific competition? *Canadian Journal of Zoology* **63**(9), 2134-2140.

Brown GP, Phillips BL, Webb JK, Shine R (2006) Toad on the road: Use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation* **133**(1), 88-94.

Brown K, Moller H, Innes J, Alterio N (1996) Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. *New Zealand Journal of Ecology* **20**(2), 271-276.

Bruemmer C, Lurz P, Larsen K, Gurnell J (2000) Impacts and management of the alien eastern gray squirrel in Great Britain and Italy: lessons for British Columbia. In 'Proceedings of a conference on the biology and management of species and habitats at risk. Vol. 1.' Ed. LM Darling) pp. 341-349. (B.C. Ministry of Environment, Lands and Parks, Victoria, British Columbia, and University College of the Cariboo, Kamloops, British Columbia)

Bryce J, Johnson PJ, Macdonald DW (2002) Can niche use in red and grey squirrels offer clues for their apparent coexistence? *Journal of Applied Ecology* **39**(6), 875-887.

Bryce JM, Speakman JR, Johnson PJ, Macdonald DW (2001) Competition between Eurasian red and introduced eastern grey squirrels: the energetic significance of body mass differences. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**(1477), 1731.

Bryce R, Oliver MK, Davies L, Gray H, Urquhart J, Lambin X (2011) Turning back the tide of American mink invasion at an unprecedented scale through community participation and adaptive management. *Biological Conservation* **144**(1), 575-583.

Burgman MA, Fox JC (2003) Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Animal Conservation* **6**(1), 19-28.

Carere C, van Oers K (2004) Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. *Physiology & Behavior* **82**(5), 905-912.

Carey M, Hamilton G, Poole A, Lawton C (2007) The Irish squirrel survey 2007. COFORD, Dublin, Ireland. Available from: http://www.coford.ie/media/coford/content/publications/projectreports/irishsquirrelsurvey2007revised.pdf.

Caswell H, Lensink R, Neubert MG (2003) Demography and dispersal: life table response experiments for invasion speed. *Ecology* **84**(8), 1968-1978.

Catling PC, Burt RJ, Kooyman R (1997) A comparison of techniques used in a survey of the ground-dwelling and arboreal mammals in forests in north-eastern New South Wales. *Wildlife Research* **24**(4), 417-432.

Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioral and personality traits influence the success of unintentional species introductions? *Trends in Ecology & Evolution* **27**(1), 57-64.

Clavero M, Brotons L, Pons P, Sol D (2009) Prominent role of invasive species in avian biodiversity loss. *Biological Conservation* **142**(10), 2043-2049.

Cohn JP (2008) Citizen science: Can volunteers do real research? *BioScience* **58**(3), 192-197.

Converse SJ, Moore CT, Armstrong DP (2013) Demographics of reintroduced populations: Estimation, modeling, and decision analysis. *The Journal of Wildlife Management* **77**(6), 1081-1093.

Cooper CB, Dickinson J, Phillips T, Bonney R (2007) Citizen science as a tool for conservation in residential ecosystems. *Ecology and Society* **12**(2), 11 [Online] URL: http://www.ecologyandsociety.org/vol12/iss2/art11/.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A (2010a) Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1560), 4065-4076.

Cote J, Dreiss A, Clobert J (2008) Social personality trait and fitness. *Proceedings of the Royal Society B: Biological Sciences* **275**(1653), 2851-2858.

Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A (2010b) Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B: Biological Sciences* **277**(1687), 1571-1579.

Courchamp F, Chapuis JL, Pascal M (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews* **78**(3), 347-383.

Creel S, Christianson D, Liley S, Winnie JA (2007) Predation risk affects reproductive physiology and demography of elk. *Science* **315**(5814), 960.

Crooks JA (2005) Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience* **12**(3), 316-329.

Croose E, Birks JDS, Schofield HW (2013) Expansion zone survey of pine marten (*Martes martes*) distribution in Scotland. Scottish Natural Heritage Commissioned Report No. 520.

Crosbie SP, Koenig WD, Reisen WK, Kramer VL, Marcus L, Carney R, Pandolfino E, Bolen GM, Crosbie LR, Bell DA, Ernest HB (2008) Early impact of the West Nile virus on the yellow-billed magpie (*Pica nuttalli*). *The Auk* **125**(3), 542-550.

CSO (2011) 'Population of each province, county and city, 2011.' Central Statistics Office Available at: http://www.cso.ie/en/statistics/population/populationofeachprovincecountyandcity2011/ Accessed: 30 October 2013.

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**(1), 63-87.

Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters* **7**(8), 734-739.

Dammhahn M (2012) Are personality differences in a small iteroparous mammal maintained by a life-history trade-off? *Proceedings of the Royal Society B: Biological Sciences* **279**(1738), 2645-2651.

Davis MA, Thompson K (2000) Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* **81**(3), 226-230.

Davis MA, Thompson K, Grime JP (2001) Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions* **7**(1-2), 97-102.

Davis MA, Thompson K, Philip Grime J (2005) Invasibility: the local mechanism driving community assembly and species diversity. *Ecography* **28**(5), 696-704.

Delaney D, Sperling C, Adams C, Leung B (2008) Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions* **10**(1), 117-128.

Devictor V, Whittaker RJ, Beltrame C (2010) Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions* **16**(3), 354-362.

Dewsbury DA (1982) Dominance rank, copulatory behavior, and differential reproduction. *The Quarterly Review of Biology* **57**(2), 135-159.

Di Febbraro M, Lurz PWW, Genovesi P, Maiorano L, Girardello M, Bertolino S (2013) The use of climatic niches in screening procedures for introduced species to evaluate risk of spread: a case with the American eastern grey squirrel. *PLoS ONE* **8**(7), e66559.

Dickinson J, Zuckerberg B, Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. *Annual review of ecology, evolution, and systematics* **41**(1), 149-172.

Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ (2005) Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution* **20**(9), 470-474.

Dingemanse NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**(1541), 847-852.

Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ (2003) Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**(1516), 741-747.

Dingemanse NJ, Réale D (2005) Natural selection and animal personality. *Behaviour* **142**(9-10), 9-10.

Dingemanse NJ, Wolf M (2010) Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1560), 3947-3958.

Doebel JH, McGinnes BS (1974) Home range and activity of a gray squirrel population. *The Journal of Wildlife Management* **38**(4), 860-867.

Doherty PF, White GC, Burnham KP (2012) Comparison of model building and selection strategies. *Journal of Ornithology* **152**(2), 317-323.

Don BAC (1983) Home range characteristics and correlates in tree squirrels. *Mammal Review* **13**(2-4), 123-132.

Drake JM, Bossenbroek JM (2004) The potential distribution of zebra mussels in the United States. *BioScience* **54**(10), 931-941.

Dubock AC (1979) Male grey squirrel (*Sciurus carolinensis*) reproductive cycles in Britain. *Journal of Zoology* **188**(1), 41-51.

Duckworth RA, Badyaev AV (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences* **104**(38), 15017-15022.

Duckworth RA, Kruuk LEB (2009) Evolution of genetic integration between dispersal and colonization ability in a bird. *Evolution* **63**(4), 968-977.

Dunn JC, Cole EF, Quinn JL (2011) Personality and parasites: sex-dependent associations between avian malaria infection and multiple behavioural traits. *Behavioral Ecology and Sociobiology* **65**(7), 1459-1471.

Dunning JB, Jr., Stewart DJ, Danielson BJ, Noon BR, Root TL, Roland HL, Stevens EE (1995) Spatially explicit population models: current forms and future uses. *Ecological Applications* **5**(1), 3-11.

EEA (2007) CLC2006 Technical Guidelines. Office for Official Publications of the European Communities, Luxembourg.

Elton CS (1958) 'The ecology of invasions by animals and plants.' (The University of Chicago Press: Chicago)

EPA (2003) Irish waterways data. Environmental Protection Agency: Wexford, Ireland

Eraud C, Boutin J-M, Roux D, Faivre B (2007) Spatial dynamics of an invasive bird species assessed using robust design occupancy analysis: the case of the Eurasian collared dove (*Streptopelia decaocto*) in France. *Journal of Biogeography* **34**(6), 1077-1086.

Erhard HW, Mendl M, Christiansen SB (1999) Individual differences in tonic immobility may reflect behavioural strategies. *Applied Animal Behaviour Science* **64**(1), 31-46.

Fagerstone KA, Miller LA, Killian G, Yoder CA (2010) Review of issues concerning the use of reproductive inhibitors, with particular emphasis on resolving human-wildlife conflicts in North America. *Integrative Zoology* **5**(1), 15-30.

Fasola L, Muzio J, Chehébar C, Cassini M, Macdonald DW (2011) Range expansion and prey use of American mink in Argentinean Patagonia: dilemmas for conservation. *European Journal of Wildlife Research* **57**(2), 283-294.

Ferrari C, Pasquaretta C, Carere C, Cavallone E, von Hardenberg A, Réale D (2013) Testing for the presence of coping styles in a wild mammal. *Animal Behaviour* **85**(6), 1385-1396.

Ferryman M, Mayle BA, Morgan GW (2006) Visual method for evaluating the state of sexual development in male grey squirrels (*Sciurus carolinensis*). *Reproduction, Fertility and Development* **18**(3), 383-393.

Fimbel C, Freed S (2008) Monitoring western gray squirrels for landscape management in western Washington. *Northwest Science* **82**(4), 299-308.

Finnegan L, Hamilton G, Perol J, Rochford J (2007) The use of hair tubes as an indirect method for monitoring red and grey squirrel populations. *Biology and Environment: Proceedings of the Royal Irish Academy* **107B**(2), 55-60.

Fischer RA, Holler NR (1991) Habitat use and relative abundance of gray squirrels in southern Alabama. *The Journal of Wildlife Management* **55**(1), 52-59.

Fitzgibbon CD (1993) The distribution of grey squirrel dreys in farm woodland: the influence of wood area, isolation and management. *Journal of Applied Ecology* **30**(4), 736-742.

Florance D, Webb JK, Dempster T, Kearney MR, Worthing A, Letnic M (2011) Excluding access to invasion hubs can contain the spread of an invasive vertebrate. *Proceedings of the Royal Society B: Biological Sciences* **278**(1720), 2900-2908.

Fogarty S, Cote J, Sih A (2011) Social personality polymorphism and the spread of invasive species: a model. *The American Naturalist* **177**(3), 273-287.

Forsyth DM, Duncan RP, Bomford M, Moore G (2004) Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. *Conservation Biology* **18**(2), 557-569.

FS (2007) Forest07 data. Forest Service; Department of Agriculture, Food and the Marine: Dublin, Ireland

Fujisaki I, Pearlstine EV, Mazzotti FJ (2010) The rapid spread of invasive Eurasian collared doves *Streptopelia decaocto* in the continental USA follows human-altered habitats. *Ibis* **152**(3), 622-632.

Fukami T, Wardle DA, Bellingham PJ, Mulder CPH, Towns DR, Yeates GW, Bonner KI, Durrett MS, Grant-Hoffman MN, Williamson WM (2006) Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters* **9**(12), 1299-1307.

Gaidet-Drapier N, Fritz H, Bourgarel M, Renaud P-C, Poilecot P, Chardonnet P, Coid C, Poulet D, Bel S (2006) Cost and efficiency of large mammal census techniques: comparison of methods for a participatory approach in a communal area, Zimbabwe. *Biodiversity & Conservation* **15**(2), 735-754.

Galloway AWE, Tudor MT, Vander Haegen WM (2006) The reliability of citizen science: a case study of Oregon white oak stand surveys. *Wildlife Society Bulletin* **34**(5), 1425-1429.

Garamszegi LZ, Eens M, Török J (2009) Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. *Animal Behaviour* **77**(4), 803-812.

Garden JG, McAlpine CA, Possingham HP, Jones DN (2007) Using multiple survey methods to detect terrestrial reptiles and mammals: what are the most

successful and cost-efficient combinations? *Wildlife Research* **34**(3), 218-227.

Goheen JR, Swihart RK, Gehring TM, Miller MS (2003) Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos* **102**(1), 95-103.

Goldstein EA, Lawton C, Sheehy E, Butler F (2014) Locating species range frontiers: a cost and efficiency comparison of citizen science and hair-tube survey methods for use in tracking an invasive squirrel. *Wildlife Research* **41**(1), 64-75.

Gonzales EK (2005) The distribution and habitat selection of introduced eastern grey squirrels, *Sciurus carolinensis*, in British Columbia. *The Canadian Field-Naturalist* **119**(3), 343-350.

Goodman SJ, Barton NH, Swanson G, Abernethy K, Pemberton JM (1999) Introgression through rare hybridization: a genetic study of a hybrid zone between red and sika deer (genus *Cervus*) in Argyll, Scotland. *Genetics* **152**(1), 355-371.

Gorman OT, Roland RR (1989) Consequences of a temporally and spatially variable food supply for an unexploited gray squirrel (*Sciurus carolinensis*) population. *American Midland Naturalist* **121**(1), 41-60.

Gosling LM, Baker SJ (1989) The eradication of muskrats and coypus from Britain. *Biological Journal of the Linnean Society* **38**(1), 39-51.

Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. *Neuroscience & Biobehavioral Reviews* **29**(1), 137-150.

Guichón ML, Doncaster CP (2008) Invasion dynamics of an introduced squirrel in Argentina. *Ecography* **31**(2), 211-220.

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19**(9), 470-474.

Gurnell J (1983) Squirrel numbers and the abundance of tree seeds. *Mammal Review* **13**(2/3/4), 133-148.

Gurnell J (1987) 'The natural history of squirrels.' (Facts on File, Inc: New York)

Gurnell J (1993) Tree seed production and food conditions for rodents in an oak wood in southern England. *Forestry* **66**(3), 291-315.

Gurnell J (1996) The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *Journal of Applied Ecology* **33**(2), 325-338.

Gurnell J, Clark MJ, Lurz PWW, Shirley MDF, Rushton SP (2002) Conserving red squirrels (*Sciurus vulgaris*): mapping and forcasting habitat suitability using a geographic information systems approach. *Biological Conservation* **105**(1), 53-64.

Gurnell J, Kenward RE, Pepper H, Lurz PWW (2008a) Grey squirrel. In 'Mammals of the British Isles: handbook.' 4th edition edn. (Eds S Harris and DW Yalden) pp. 66-72. (The Mammal Society: Southampton)

Gurnell J, Lurz P, McDonald R, Pepper H (2009) Practical techniques for surveying and monitoring squirrels. Forestry Commission, No. FCPN011. 1-12.

Gurnell J, Lurz PWW, Halliwell EC (2008b) Red squirrel. In 'Mammals of the British Isles: handbook.' 4th edn. (Eds S Harris and DW Yalden) pp. 56-66. (The Mammal Society: Southampton)

Gurnell J, Lurz PWW, Shirley MDF, Cartmel S, Garson PJ, Magris L, Steele J (2004a) Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain. *Mammal Review* **34**(1-2), 51-74.

Gurnell J, Pepper H (1993) A critical look a conserving the British red squirrel *Sciurus vulgaris*. *Mammel Review* **23**(3/4), 127-137.

Gurnell J, Rushton SP, Lurz PWW, Sainsbury AW, Nettleton P, Shirley MDF, Bruemmer C, Geddes N (2006) Squirrel poxvirus: landscape scale strategies for managing disease threat. *Biological Conservation* **131**(2), 287-295.

Gurnell J, Wauters LA, Lurz PWW, Tosi G (2004b) Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *Journal of Animal Ecology* **73**(1), 26-35.

Gurnell J, Wauters LA, Preatoni D, Tosi G (2001) Spacing behaviour, kinship, and population dynamics of grey squirrels in a newly colonized broadleaf woodland in Italy. *Canadian Journal of Zoology* **79**(9), 1533-1543.

Hale ML, Lurz PWW, Shirley MDF, Rushton S, Fuller RM, Wolff K (2001) Impact of landscape management on the genetic structure of red squirrel populations. *Science* **293**(5538), 2246-2248.

Hanski I (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, 151-162.

Harris RL, Nicol SC (2010) The effectiveness of hair traps for surveying mammals: results of a study in sandstone caves in the Tasmanian southern midlands. *Australian Mammalogy* **32**(1), 62-66.

Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A, Harrison S, Holland M, Lambrinos J, Malvadkar U, Melbourne BA, Moore K, Taylor C, Thomson D (2005) The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* **8**(1), 91-101.

Havera SP, Smith KE (1979) A nutritional comparison of selected fox squirrel foods. *The Journal of Wildlife Management* **43**(3), 691-704.

Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? *Biological Invasions* **10**(4), 483-506.

Healy WM, Welsh CJE (1992) Evaluating line transects to monitor gray squirrel populations. *Wildlife Society Bulletin* **20**(1), 83-90.

Hibbard CW (1935) Breeding seasons of gray squirrel and flying squirrel. *Journal of Mammalogy* **16**(4), 325-326.

Hickie D (1990) Forestry in Ireland - policy and practice. An Taisce, Dublin.

Higgins SI, Richardson DM, Cowling RM (1996) Modeling invasive plant spread: the role of plant-environment interactions and model structure. *Ecology* **77**(7), 2043-2054.

Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *Journal of Applied Ecology* **45**(2), 403-414.

Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105**(3), 405-412.

Hungerford KE, Wilder NG (1941) Observations on the homing behavior of the gray squirrel (*Sciurus carolinensis*). *The Journal of Wildlife Management* **5**(4), 458-460.

Hwang YT, Lariviére S (2006) A test of interspecific effects of introduced eastern grey squirrels, *Sciurus carolinensis*, on douglas's squirrels, *Tamiasciurus douglasii*, in Vancouver, British Columbia. *The Canadian Field-Naturalist* **120**(1), 10-14.

Jacob J, Herawati NA, Davis SA, Singleton GR (2004) The impact of sterilized females on enclosed populations of ricefield rats. *The Journal of Wildlife Management* **68**(4), 1130-1137.

Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America* **102**(20), 7198-7202.

Jessen RR, Merrick MJ, Koprowski JL, Ramirez O (2010) Presence of Guayaquil squirrels on the central coast of Peru: an apparent introduction. *Mammalia: International Journal of the Systematics, Biology & Ecology of Mammals* **74**(4), 443-444.

Johnson JC, Sih A (2007) Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Animal Behaviour* **74**(5), 1131-1138.

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology* **22**(1), 16-26.

Kelly DJ, Hawes I (2005) Effects of invasive macrophytes on littoral-zone productivity and foodweb dynamics in a New Zealand high-country lake. *Journal of the North American Benthological Society* **24**(2), 300-320.

Kelly J, Tosh D, Dale K, Jackson A (2013) The economic cost of invasive and non-native species in Ireland and Northern Ireland., A report prepared for the Northern Ireland Environment Agency and National Parks and Wildlife Service as part of Invasive Species Ireland.

Kenward R, Parish T (1986) Bark-stripping by grey squirrels (*Sciurus carolinensis*). *Journal of Zoology* **210**(3), 473-481.

Kenward R, Tonkin J (1986) Red and grey squirrels: some behavioural and biometric differences. *Journal of Zoology* **209**(2), 279-281.

Kenward RE (1985) Ranging behaviour and populations dynamics in grey squirrels. In 'Behavioural ecology: ecological consequences of adaptive behaviour.' (Eds RM Sibly and RH Smith) pp. 319-330. (Blackwell Scientific Publications: Oxford, UK)

Kenward RE (1989) Bark stripping by grey squirrel in Britain and North America: Why does the damage differ? In 'Mammals as Pests.' Ed. R Putman) pp. 144-153. (Chapman and Hall Ltd.: London)

Kenward RE, Hodder KH (1998) Red squirrels (*Sciurus vulgaris*) released in conifer woodland: the effects of source habitat, predation and interactions with grey squirrels (*Sciurus carolinensis*). *Journal of Zoology* **244**(1), 23-32.

Kenward RE, Hodder KH, Rose RJ, Walls CA, Parish T, Holm JL, Morris PA, Walls SS, Doyle FI (1998) Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. *Journal of Zoology* **244**(1), 7-21.

Kenward RE, Holm JL (1993) On the replacement of the red squirrel in Britain. A phytotoxic explanation. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **251**(1332), 187-194.

Kimbro D, Grosholz E, Baukus A, Nesbitt N, Travis N, Attoe S, Coleman-Hulbert C (2009) Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. *Oecologia* **160**(3), 563-575.

Kirkman TW (1996) 'Statistics to use.' Available at: http://www.physics.csbsju.edu/stats Accessed: 20 November 2012.

Koenig WD, Marcus L, Scott TW, Dickinson JL (2007) West Nile virus and California breeding bird declines. *EcoHealth* **4**(1), 18-24.

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**(4), 199-204.

Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. *Science* **298**(5596), 1233-1236.

Koolhaas JM, Meerlo P, de Boer SF, Strubbe JH, Bohus B (1997) The temporal dynamics of the stress response. *Neuroscience & Biobehavioral Reviews* **21**(6), 775-782.

Koprowski JL (1991) Response of fox squirrels and gray squirrels to a late spring-early summer food shortage. *Journal of Mammalogy* **72**(2), 367-372.

Koprowski JL (1992) Removal of copulatory plugs by female tree squirrels. *Journal of Mammalogy* **73**(3), 572-576.

Koprowski JL (1993) Alternative reproductive tactics in male eastern gray squirrels: "making the best of a bad job". *Behavioral Ecology* **4**(2), 165-171.

Koprowski JL (1994) *Sciurus carolinensis*. *Mammalian Species* **480**, 1-9.

Koprowski JL (1996) Natal philopatry, communal nesting, and kinship in fox squirrels and gray squirrels. *Journal of Mammalogy* **77**(4), 1006-1016.

Koprowski JL (2005) The response of tree squirrels to fragmentation: a review and synthesis. *Animal Conservation* **8**(4), 369-376.

Korschgen LJ (1981) Foods of Fox and Gray Squirrels in Missouri. *The Journal of Wildlife Management* **45**(1), 260-266.

Korsten P, Mueller JC, Hermannstaedter C, Bouwman KM, Dingemanse NJ, Drent PJ, Liedvogel M, Matthysen E, van Oers K, van Overveld T (2010) Association between DRD4 gene polymorphism and personality variation in great tits: a test across four wild populations. *Molecular Ecology* **19**(4), 832-843.

Krause SK, Kelt DA, Gionfriddo JP, Van Vuren DH (2014) Efficacy and health effects of a wildlife immunocontraceptive vaccine on fox squirrels. *The Journal of Wildlife Management* **78**(1), 12-23.

Kyle A (2009) A comparison of grey squirrel (*Sciurus carolinensis*) densities between an urban park and semi-rural woodland in Glasgow. *Glasgow Naturalist* **25**(2), 23-26.

LaDeau SL, Kilpatrick AM, Marra PP (2007) West Nile virus emergence and large-scale declines of North American bird populations. *Nature* **447**(7145), 710-713.

Lane JE, Boutin S, Gunn MR, Coltman DW (2009) Sexually selected behaviour: red squirrel males search for reproductive success. *Journal of Animal Ecology* **78**(2), 296-304.

Larson BM (2005) The war of the roses: demilitarizing invasion biology. *Frontiers in Ecology and the Environment* **3**(9), 495-500.

Lauber TB, Knuth BA (2004) Effects of information on attitudes toward suburban deer management. *Wildlife Society Bulletin* **32**(2), 322-331.

Lawton C (1999) Grey squirrel, *Sciurus carolinensis*, ecology in managed broadleaved woodland. Ph.D Thesis, Trinity College Dublin, Dublin

Lawton C (2003) Controlling grey squirrel damage in Irish broadleaved woodlands. Dublin. 1-6.

Lawton C, Cowan P, Bertolino S, Lurz PWW, Peters AR (2010) The consequences of introducing non-indigenous species: two case studies, the grey squirrel in Europe and the brushtail possum in New Zealand. *Revue Scientifique et Technique - Office International des Epizooties* **29**(2), 287-298.

Lawton C, Flaherty M, Goldstein EA, Sheehy E, Carey M (*In prep.*) All Ireland squirrel survey 2012 *(provisional title and author order)*.

Lawton C, Rochford J (2007) The recovery of grey squirrel (*Sciurus carolinensis*) populations after intensive control programmes. *Biology and Environment: Proceedings of the Royal Irish Academy* **107**, 19-29.

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological monographs* **62**(1), 67-118.

Lessells C, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. *The Auk*, 116-121.

Leung B, Finnoff D, Shogren JF, Lodge D (2005) Managing invasive species: rules of thumb for rapid assessment. *Ecological Economics* **55**(1), 24-36.

Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society B: Biological Sciences* **269**, 2407-2413.

Lindstedt S, Calder III W (1981) Body size, physiological time, and longevity of homeothermic animals. *Quarterly Review of Biology* **56**(1), 1-16.

Lishak RS (1982) Vocalizations of nestling gray squirrels. *Journal of Mammalogy* **63**(3), 446-452.

Lishak RS (1984) Alarm vocalizations of adult gray squirrels. *Journal of Mammalogy* **65**(4), 681-684.

Llewelyn J, Phillips B, Alford R, Schwarzkopf L, Shine R (2010) Locomotor performance in an invasive species: cane toads from the invasion front have greater endurance, but not speed, compared to conspecifics from a long-colonised area. *Oecologia* **162**(2), 343-348.

Lockwood JL, Hoopes MF, Marchetti MP (2007) 'Invasion Ecology.' (Blackwell Publishing: Malden, Massachusetts)

Lodge DM, Shrader-Frechette K (2003) Nonindigenous species: ecological explanation, environmental ethics, and public policy. *Conservation Biology* **17**(1), 31-37.

Long J (2003) 'Introduced mammals of the world: their history, distribution and influence.' (Csiro Publishing: Collingwood, Australia)

Longley WH (1963) Minnesota gray and fox squirrels. *American Midland Naturalist* **69**(1), 82-98.

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**(5), 1522-1536.

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species a selection from the global invasive species database. Gland, Switzerland.

Lurz P, Koprowski J, Wood D (2008) The use of GIS and modelling approaches in squirrel population management and conservation: a review. *Current Science* **95**(7), 918-922.

Lurz PWW, Garson PJ, Rushton SP (1995) The ecology of squirrels in spruce dominated plantations: implications for forest management. *Forest Ecology and Management* **79**(1-2), 79-90.

Lurz PWW, Garson PJ, Wauters LA (2000) Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). *Journal of Zoology* **251**, 167-178.

Lurz PWW, Gurnell J, Magris L (2005) *Sciurus vulgaris*. *Mammalian Species* **769**, 1-10.

Lurz PWW, Lloyd AJ (2000) Body weights in grey and red squirrels: do seasonal weight increases occur in conifer woodland? *Journal of Zoology* **252**(4), 531-547.

Lurz PWW, Rushton SP, Wauters LA, Bertolino S, Currado I, P. M, Shirley MDF (2001) Predicting grey squirrel expansion in North Italy: a spacially explicit modelling approach. *Landscape Ecology* **16**(5), 407-420.

Lyra-Jorge MC, Ciocheti G, Pivello VR, Meirelles ST (2008) Comparing methods for sampling large- and medium-sized mammals: camera traps and track plots. *European Journal of Wildlife Research* **54**(4), 739-744.

Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**(3), 689-710.

MacKenzie DI (2005) What are the issues with presence-absence data for wildlife managers? *The Journal of Wildlife Management* **69**(3), 849-860.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Andrew Royle J, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**(8), 2248-2255.

MacKinnon K (1978) Competition between red and grey squirrels. *Mammal Review* **8**(4), 185-190.

Martin JG, Réale D (2008) Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour* **75**(1), 309-318.

Matsinos YG, Papadopoulou E (2004) Investigating the viability of squirrel populations; a modeling approach for the island of Lesvos, Greece. *Natural Resource Modeling* **17**(4), 423-444.

Matthysen E (2005) Density-dependent dispersal in birds and mammals. *Ecography* **28**(3), 403-416.

Mayle BA, Ferryman M, Peace A, Yoder CA, Miller L, Cowan D (2013) The use of DiazaCon™ to limit fertility by reducing serum cholesterol in female grey squirrels, *Sciurus carolinensis*. *Pest Management Science* **69**(3), 414-424.

Mayle BA, Proudfoot J, Poole J (2009) Influence of tree size and dominance on incidence of bark stripping by grey squirrels to oak and impact on tree growth. *Forestry* **82**(4), 431-444.

McDonald KA, Brown JH (1992) Using montane mammals to model extinctions due to global change. *Conservation Biology* **6**(3), 409-415.

McGeoch MA, Butchart SHM, Spear D, Marais E, Kleynhans EJ, Symes A, Chanson J, Hoffmann M (2010) Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. *Diversity and Distributions* **16**(1), 95-108.

McGoldrick M, Rochford J (2009) Recent range expansion by the grey squirrel (*Sciurus carolinensis* Gmelin 1788). *Irish Naturalists' Journal* **30**(1), 24-28.

McGoldrick MS (2011) The vagility of an invasive species, the grey squirrel (*Sciurus carolinensis*) - studies of population genetic structure, control and recolonisation, range expansion and pox virus. Ph.D Thesis, Trinity College, Dublin

McInnes CJ, Coulter L, Dagleish MP, Deane D, Gilray J, Percival A, Willoughby K, Scantlebury M, Marks N, Graham D, Everest DJ, McGoldrick M, Rochford J, McKay F, Sainsbury AW (2013) The emergence of squirrelpox in Ireland. *Animal Conservation* **16**(1), 51-59.

Mech SG, Zollner PA (2002) Using body size to predict perceptual range. *Oikos* **98**(1), 47-52.

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Josh Donlan C, Keitt BS, Le Corre M, Horwath SV, Nogales M (2011) A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology* **17**(11), 3503-3510.

Meekins JF, McCarthy BC (2002) Effect of population density on the demography of an invasive plant (*Alliaria petiolata*, Brassicaceae) population in a southeastern Ohio forest. *American Midland Naturalist* **147**(2), 256-278.

Memmott J, Craze PG, Harman HM, Syrett P, Fowler SV (2005) The effect of propagule size on the invasion of an alien insect. *Journal of Animal Ecology* **74**(1), 50-62.

Meserve PL, Yunger JA, Gutiérrez JR, Contreras LC, Milstead WB, Lang BK, Cramer KL, Herrera S, Lagos VO, Silva SI, Tabilo EL, Torrealba M-A, Jaksic FM (1995) Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. *Journal of Mammalogy* **76**(2), 580-595.

Met-Éireann (2014) 'Rainfall.' Available at: http://www.met.ie/climate-ireland/rainfall.asp Accessed: 22 April 2014.

Mills AD, Faure JM (2000) Ease of capture in lines of Japanese quail (*Coturnix japonica*) subjected to contrasting selection for fear or sociability. *Applied Animal Behaviour Science* **69**(2), 125-134.

Mills LS, Smouse PE (1994) Demographic consequences of inbreeding in remnant populations. *The American Naturalist* **144**(3), 412-431.

Montgomery SD, Whelan JB, Mosby HS (1975) Bioenergetics of a woodlot gray squirrel population. *The Journal of Wildlife Management* **39**(4), 709-717.

Montiglio P-O, Garant D, Bergeron P, Dubuc Messier G, Réale D (2014) Pulsed resources and the coupling between life-history strategies and exploration patterns in eastern chipmunks (*Tamias striatus*). *Journal of Animal Ecology*, doi: 10.1111/1365-2656.12174.

Montiglio P-O, Garant D, Pelletier F, Réale D (2012) Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour* **84**(4), 1071-1079.

Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascant foci. *Journal of Applied Ecology* **25**(3), 1009-1021.

Moore H, Jenkins N, Wong C (1997) Immunocontraception in rodents: a review of the development of a sperm-based immunocontraceptive vaccine for the grey squirrel (*Sciurus carolinensis*). *Reproduction, Fertility, and Development* **9**(1), 125-129.

Mortelliti A, Boitani L (2008) Inferring red squirrel (*Sciurus vulgaris*) absence with hair tubes surveys: a sampling protocol. *European Journal of Wildlife Research* **54**(2), 353-356.

Mortelliti A, Cervone C, Amori G, Boitani L (2010) The effect of non-target species in presence-absence distribution surveys: a case study with hair-tubes. *Italian Journal of Zoology* **77**(2), 211-215.

Mosby HS (1969) The influence of hunting on the population dynamics of a woodlot gray squirrel population. *The Journal of Wildlife Management* **33**(1), 59-73.

Myers JH, Simberloff D, Kuris AM, Carey JR (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology & Evolution* **15**(8), 316-320.

Newman G, Wiggins A, Crall A, Graham E, Newman S, Crowston K (2012) The future of citizen science: emerging technologies and shifting paradigms. *Frontiers in Ecology and the Environment* **10**(6), 298-304.

Ní Dhubháin Á, Fléchard M-C, Moloney R, O'Connor D (2009) Assessing the value of forestry to the Irish economy - an input-output approach. *Forest policy and economics* **11**(1), 50-55.

Nielsen BO (1977) Beech seeds as an ecosystem component. *Oikos* **29**(2), 268-274.

Nixon CM, Edwards WR, Eberhardt L (1967) Estimating squirrel abundance from livetrapping data. *The Journal of Wildlife Management* **31**(1), 96-101.

Nixon CM, McClain MW (1969) Squirrel population decline following a late spring frost. *The Journal of Wildlife Management* **33**(2), 353-357.

Nixon CM, McClain MW (1975) Breeding seasons and fecundity of female gray squirrels in Ohio. *The Journal of Wildlife Management* **39**(2), 426-438.

Nixon CM, McClain MW, Donohoe RW (1975) Effects of hunting and mast crops on a squirrel population. *The Journal of Wildlife Management* **39**(1), 1-25.

Nixon CM, McClain MW, Donohoe RW (1980) Effects of clear-cutting on gray squirrels. *The Journal of Wildlife Management* **44**(2), 403-412.

NPWS (1968) The distribution of red and grey squirrels in Ireland. Unpublished internal report, Office of Public Works, Dublin, Ireland. Cited in: O'Teangana DO, Reilly S, Montgomery WI, Rochford J. (2000) Distribution and status of the red squirrel (*Sciurus vulgaris*) and grey squirrel (*Sciurus carolinensis*) in Ireland. *Mammal Review* **30**(1), 45-56.

Nussey DH, Wilson AJ, Brommer JE (2007) The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology* **20**(3), 831-844.

O'Meara D, Turner P, Coffey L, O'Reilly C (2012) TaqMan assays for species identification of the red squirrel (*Sciurus vulgaris*) and the grey squirrel (*Sciurus carolinensis*). *Conservation Genetics Resources* **4**(3), 603-604.

O'Teangana D (1999) The distribution and ecology of the red squirrel (*Sciurus vulgaris*) and the grey squirrel (*Sciurus carolinensis*) in Northern Ireland. Ph.D Thesis, Queen's University, Belfast

O'Teangana DO, Reilly S, Montgomery WI, Rochford J (2000a) Distribution and status of the red squirrel (*Sciurus vulgaris*) and grey squirrel (*Sciurus carolinensis*) in Ireland. *Mammal Review* **30**(1), 45-56.

O'Teangana DO, Russ JM, Mathers RG, Montgomery WI (2000b) Habitat associations of the red squirrel *Sciurus vulgaris* and grey squirrel *S. carolinensis* in Northern Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **100B**(1), 27-33.

Okubo A, Maini PK, Williamson MH, Murray JD (1989) On the spatial spread of the grey squirrel in Britain. *Proceedings of the Royal Society of London. B. Biological Sciences* **238**(1291), 113-125.

Orrock JL, Danielson BJ (2004) Rodents balancing a variety of risks: invasive fire ants and indirect and direct indicators of predation risk. *Oecologia* **140**(4), 662-667.

Pai M, Bruner R, Schlafer DH, Yarrow GK, Yoder CA, Miller LA (2011) Immunocontraception in eastern gray squirrels (*Sciurus carolinensis*): morphologic changes in reproductive organs. *Journal of Zoo and Wildlife Medicine* **42**(4), 718-722.

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**(1), 3-19.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual review of ecology, evolution, and systematics*, 637-669.

Pascal M, Le Guyader H, Simberloff D (2010) Biological invasions and the conservation of biodiversity. *Revue Scientifique et Technique (International Office of Epizootics)* **29**(2), 387-403.

Pasitschniak-Arts M, Bendell JF (1990) Behavioural differences between locally recruiting and dispersing gray squirrels, *Sciurus carolinensis*. *Canadian Journal of Zoology - Revue Canadienne De Zoologie* **68**, 935-941.

Patterson LD, Schulte-Hostedde AI (2011) Behavioural correlates of parasitism and reproductive success in male eastern chipmunks, *Tamias striatus*. *Animal Behaviour* **81**(6), 1129-1137.

Paull DJ, Claridge AW, Cunningham RB (2012) Effective detection methods for medium-sized ground-dwelling mammals: a comparison between infrared digital cameras and hair tunnels. *Wildlife Research* **39**, 546-553.

Peacock DS, Van Rensburg BJ, Robertson MP (2007) The distribution and spread of the invasive alien common myna, *Acridotheres tristis* L. (Aves: Sturnidae), in southern Africa. *South African Journal of Science* **103**(11-12), 465-473.

Pepper H (1993) Red squirrel supplementary food hopper. Forestry Commission. Research Information Note 235.

Perry HR, Jr., Garland BP, Barkalow FS, Jr., Monroe RJ (1977) Factors affecting trap responses of the gray squirrel. *The Journal of Wildlife Management* **41**(1), 135-143.

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* **52**(3), 273-288.

Pocock MJO, Jennings N (2006) Use of hair tubes to survey for shrews: new methods for identification and quantification of abundance. *Mammal Review* **36**(4), 299-308.

Poole A, Gormally M, Sheehy Skeffington M (2003) The flora and carabid beetle fauna of a mature and regenerating semi-natural oak woodland in south-east Ireland. *Forest Ecology and Management* **177**(1), 207-220.

Poole A, Lawton C (2009) The translocation and post release settlement of red squirrels *Sciurus vulgaris* to a previously uninhabited woodland. *Biodiversity and Conservation* **18**(12), 3205-3218.

Powell LA (2007) Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* **109**(4), 949-954.

Quinn JL, Cole EF, Patrick SC, Sheldon BC (2011) Scale and state dependence of the relationship between personality and dispersal in a great tit population. *Journal of Animal Ecology* **80**(5), 918-928.

Quinn JL, Patrick SC, Bouwhuis S, Wilkin TA, Sheldon BC (2009) Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology* **78**(6), 1203-1215.

Réale D, Gallant BY, Leblanc M, Festa-Bianchet M (2000) Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour* **60**(5), 589-597.

Réale D, Martin J, Coltman DW, Poissant J, Festa-Bianchet M (2009) Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology* **22**(8), 1599-1607.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**(2), 291-318.

Rehage JS, Sih A (2004) Dispersal behavior, boldness, and the link to invasiveness: a comparison of four *Gambusia* species. *Biological Invasions* **6**(3), 379-391.

Reiners TE, Encarnação JA, Wolters V (2011) An optimized hair trap for non-invasive genetic studies of small cryptic mammals. *European Journal of Wildlife Research* **57**(4), 991-995.

Richardson DM, Pyšek P (2008) Fifty years of invasion ecology - the legacy of Charles Elton. *Diversity and Distributions* **14**(2), 161-168.

Roberts NJ (2011) Investigation into survey techniques of large mammals: surveyor competence and camera-trapping vs. transect-sampling. *Bioscience Horizons* **4**(1), 40-49.

Robinson D, Cowan IM (1954) An introduced population of the gray squirrel (*Sciurus carolinensis* Gmelin) in British Columbia. *Canadian Journal of Zoology* **32**(3), 261-282.

Ruis MAW, te Brake JHA, van de Burgwal JA, de Jong IC, Blokhuis HJ, Koolhaas JM (2000) Personalities in female domesticated pigs: behavioural and physiological indications. *Applied Animal Behaviour Science* **66**(1-2), 31-47.

Rushton S, Lurz PWW, South AB, Mitchell-Jones A (1999) Modelling the distribution of red squirrels (*Sciurus vulgaris*) on the Isle of Wight. *Animal Conservation* **2**(2), 111-120.

Rushton SP, Gurnell J, Lurz PWW, Fuller RM (2002) Modeling impacts and costs of grey squirrel control regimes on the viability of red squirrel populations. *Journal of Wildlife Management* **66**(3), 683-697.

Rushton SP, Lurz PWW, Fuller R, Garson PJ (1997) Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *Journal of Applied Ecology* **34**, 1137-1154.

Rushton SP, Lurz PWW, Gurnell J, Fuller R (2000) Modelling the spatial dynamics of parapoxvirus disease in the red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *Journal Of Applied Ecology* **37**, 997-1012.

Rushton SP, Wood DJA, Lurz PWW, Koprowski JL (2006) Modelling the population dynamics of the Mt. Graham red squirrel: Can we predict its future in a changing environment with multiple threats? *Biological Conservation* **131**(1), 121-131.

Russell JC, Abdelkrim J, Fewster RM (2009) Early colonisation population structure of a Norway rat island invasion. *Biological Invasions* **11**(7), 1557-1567.

Sachot S, Perrin N (2004) Capercaillie (*Tetrao urogallus*) in western Switzerland: viability and management of an endangered grouse population. In 'Species conservation and management: case studies.' (Eds HR Akçakaya, MA Burgman, O Kindvall, CC Wood, P Sjögren-Gulve, JS Hatfield and MA McCarthy) pp. 384-396. (Oxford University Press: New York)

Sainsbury A, Deaville R, Lawson B, Cooley W, Farelly S, Stack M, Duff P, McInnes C, Gurnell J, Russell P, Rushton S, Pfeiffer D, Nettleton P, Lurz P (2008) Poxviral disease in red squirrels *Sciurus vulgaris*; in the UK: spatial and temporal trends of an emerging threat. *EcoHealth* **5**(3), 305-316.

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* **32**, 305-332.

Scantlebury M, Maher McWilliams M, Marks NJ, Dick JTA, Edgar H, Lutermann H (2010) Effects of life-history traits on parasite load in grey squirrels. *Journal of Zoology* **282**(4), 246-255.

Schuett W, Tregenza T, Dall SRX (2010) Sexual selection and animal personality. *Biological Reviews* **85**(2), 217-246.

Schwagmeyer PL, Woontner SJ (1986) Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioral Ecology and Sociobiology* **19**(5), 359-364.

Schwingel H, Norment C (2010) Use of hair tubes to detect small-mammal winter activity in a northern forest habitat. *Northeastern Naturalist* **17**(4), 531-540.

Scotts D, Craig S (1988) Improved hair-sampling tube for the detection of rare mammals. *Wildlife Research* **15**(4), 469-472.

Shaw MW (1968) Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in north Wales: I. a preliminary study of acorn production, viability and losses. *Journal of Ecology* **56**(2), 565-583.

Sheehy E (2013) The role of the pine marten in Irish squirrel population dynamics. Ph.D Thesis, National University of Ireland, Galway,

Sheehy E, Lawton C (2014) Population crash in an invasive species following the recovery of a native predator: the case of the American grey squirrel and the European pine marten in Ireland. *Biodiversity and Conservation* **23**, 753-774.

Sherman PW (1977) Nepotism and the evolution of alarm calls. *Science* **197**(4310), 1246-1253.

Shields WM (1980) Ground squirrel alarm calls: nepotism or parental care? *The American Naturalist* **116**(4), 599-603.

Shorten M (1954) 'Squirrels.' (Collins: London)

Signorile AL, Evans J (2007) Damage caused by the American grey squirrel (*Sciurus carolinensis*) to agricultural crops, poplar plantations and semi-natural woodland in Piedmont, Italy. *Forestry* **80**(1), 89-98.

Sih A, Bell A, Johnson JC (2004a) Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**(7), 372-378.

Sih A, Bell AM, Johnson JC, Ziemba RE (2004b) Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology* **79**(3), 241-277.

Sih A, Cote J, Evans M, Fogarty S, Pruitt J (2012) Ecological implications of behavioural syndromes. *Ecology Letters* **15**(3), 278-289.

Silvertown J (2009) A new dawn for citizen science. *Trends in Ecology and Evolution* **24**(9), 467-471.

Simberloff D (2003) How much information on population biology is needed to manage introduced species? *Conservation Biology* **17**(1), 83-92.

Simberloff D (2009) Rats are not the only introduced rodents producing ecosystem impacts on islands. *Biological Invasions* **11**(7), 1735-1742.

Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* **38**(1/2), 196-218.

Smith BR, Blumstein DT (2008) Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* **19**(2), 448-455.

Smith NB, Barkalow FS, Jr. (1967) Precocious breeding in the gray squirrel. *Journal of Mammalogy* **48**(2), 328-330.

Smith S (2001) The national inventory of woodland and trees - England. Forestry Commission UK, Edinburgh.

Smith S, Gilbert J (2003) National inventory of woodland and trees: Great Britain. Forestry Commision UK, Edinburgh.

Southwell DM, Lechner AM, Coates T, Wintle BA (2008) The sensitivity of population viability analysis to uncertainty about habitat requirements: implications for the management of the endangered southern brown bandicoot. *Conservation Biology* **22**(4), 1045-1054.

Stanley TR, Royle JA (2005) Estimating site occupancy and abundance using indirect detection indices. *Journal of Wildlife Management* **69**(3), 874-883.

Steele MA, Koprowski JL (2001) 'North American tree squirrels.' (Smithsonian Insitution: Washington DC)

Stenseth NC, Falck W, Bjørnstad ON, Krebs CJ (1997) Population regulation in snowshoe hare and Canadian lynx: Asymmetric food web configurations between hare and lynx. *Proceedings of the National Academy of Sciences* **94**(10), 5147-5152.

Sweetapple P, Fraser K, Knightbridge P (2004) Diet and impacts of brushtail possum populations across an invasion front in South Westland, New Zealand. *New Zealand Journal of Ecology* **28**(1), 19-33.

Tattoni C, Preatoni DG, Lurz PWW, Rushton SP, Tosi G, Bertolino S, Martinoli A, Wauters LA (2006) Modelling the expansion of a grey squirrel population: implications for squirrel control. *Biological Invasions* **8**(8), 1605-1619.

Taylor MK, Demaster DP, Bunnell FL, Schweinsburg RR (1987) Modeling the sustainable harvest of female polar bears. *Journal of Wildlife Management* **51**(4), 811-820.

Taylor R, Boon A, Dantzer B, Réale D, Humphries M, Boutin S, Gorrell J, Coltman D, McAdam A (2012) Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. *Journal of Evolutionary Biology* **25**(4), 614-624.

Teacher AGF, Griffiths DJ, Hodgson DJ, Inger R (2013) Smartphones in ecology and evolution: a guide for the app-rehensive. *Ecology and Evolution* **3**(16), 5268-5278.

Teerink BJ (1991) 'Hair of west-European mammals.' (Cambridge University Press: Cambridge, UK)

Tessier AJ, Leibold MA, Tsao J (2000) A fundamental trade-off in resource exploitation by daphnia and consequences to plankton communities. *Ecology* **81**(3), 826-841.

Thompson DC (1978a) Regulation of a northern grey squirrel (*Sciurus carolinensis*) population. *Ecology* **59**(4), 708-715.

Thompson DC (1978b) The social system of the grey squirrel. *Behaviour* **64**(3/4), 305-328.

Thorington Jr RW, Koprowski JL, Steele MA, Whatton JF (2012) 'Squirrels of the world.' (The Johns Hopkins University Press: Baltimore, Maryland)

Tompkins DM, White AR, Boots M (2003) Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecology Letters* **6**, 189-196.

Tonkin M, Mackenzie I (2011) The evaluation of grey squirrel control in the saving Scotland's red squirrels partnership project 2009-2011. Scottish Wildlife Trust, Edinburgh, Scotland.

Tounzen MR, Epperson D, Taulman JF (2012) Home range and habitat selection of eastern gray squirrels (*Sciurus carolinensis*) in a small urban hardwood forest. *Transactions of the Kansas Academy of Science* **115**(3/4), 89-101.

Tulloch A, Possingham HP, Wilson K (2011) Wise selection of an indicator for monitoring the success of management actions. *Biological Conservation* **144**(1), 141-154.

Tulloch AI, Possingham HP, Joseph LN, Szabo J, Martin TG (2013a) Realising the full potential of citizen science monitoring programs. *Biological Conservation* **165**, 128-138.

Tulloch AIT, Mustin K, Possingham HP, Szabo JK, Wilson KA (2013b) To boldly go where no volunteer has gone before: predicting volunteer activity to prioritize surveys at the landscape scale. *Diversity and Distributions* **19**(4), 465-480.

Tulloch AIT, Szabo JK (2012) A behavioural ecology approach to understand volunteer surveying for citizen science datasets. *Emu* **112**(4), 313-325.

Urban MC, Phillips BL, Skelly DK, Shine R (2008) A toad more traveled: the heterogeneous invasion dynamics of cane toads in Australia. *The American Naturalist* **171**(3), E134-E148.

van der Merwe M, Brown JS, Jackson WM (2005) The coexistence of fox (*Sciurus niger*) and gray (*S. carolinensis*) squirrels in the Chicago metropolitan area. *Urban Ecosystems* **8**(3-4), 335-347.

van Oers K, Drent P, De Jong G, Van Noordwijk A (2004a) Additive and nonadditive genetic variation in avian personality traits. *Heredity* **93**(5), 496-503.

van Oers K, Drent PJ, de Goede P, van Noordwijk AJ (2004b) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **271**(1534), 65-73.

Vander Haegen WM, Orth GR, Linders MJ (2013) Survival and causes of mortality in a northern population of western gray squirrels. *The Journal of Wildlife Management* **77**(6), 1249-1257.

Verbeylen G, Wauters LA, De Bruyn L, Matthysen E (2009) Woodland fragmentation affects space use of Eurasian red squirrels. *Acta Oecologica* **35**(1), 94-103.

Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**(1), 1-16.

Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological monographs* **59**(3), 247-265.

Vuilleumier S, Buttler A, Perrin N, Yearsley JM (2011) Invasion and eradication of a competitively superior species in heterogeneous landscapes. *Ecological Modelling* **222**(3), 398-406.

Ward AW, Thomas P, Hart PB, Krause J (2004) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology* **55**(6), 561-568.

Waters C, Lawton C (2011) Red squirrel translocation in Ireland. Irish Wildlife Manuals. National Parks and Wildlife Service, Department of the Environment, Heritage and Local Government Dublin, Ireland.

Watt HB (1923) The American grey squirrel in Ireland. *Irish Naturalist* **32**, 95.

Wauters L, Dhondt AA (1989) Body weight, longevity and reproductive success in red squirrels (*Sciurus vulgaris*). *The Journal of Animal Ecology* **58**(2), 637-651.

Wauters L, Dhondt AA, De Vos R (1990) Factors affecting male mating success in red squirrels (*Sciurus vulgaris*). *Ethology Ecology & Evolution* **2**(2), 195-204.

Wauters L, Tosi G, Gurnell J (2005) A review of the competitive effects of alien grey squirrels on behaviour, activity and habitat use of red squirrels in mixed, deciduous woodland in Italy. *Hystrix-the Italian Journal of Mammalogy* **16**(1).

Wauters LA, Dhondt AA (1993) Immigration pattern and success in red squirrels. *Behahavioral Ecology and Sociobiology* **33**(3), 159-167.

Wauters LA, Dhondt AA (1995) Lifetime reproductive success and its correlates in female Eurasian red squirrels. *Oikos* **72**(3), 402-410.

Wauters LA, Githiru M, Bertolino S, Molinari A, Tosi G, Lens L (2008) Demography of alpine red squirrel populations in relation to fluctuations in seed crop size. *Ecography* **31**(1), 104-114.

Wauters LA, Gurnell J (1999) The mechanism of replacement of red squirrels by grey squirrels: a test of the interference competition hypothesis. *Ethology* **105**(12), 1053-1071.

Wauters LA, Gurnell J, Martinoli A, Tosi G (2001) Does interspecific competition with introduced grey squirrels affect foraging and food choice of Eurasian red squirrels? *Animal Behaviour* **61**(6), 1079-1091.

Wauters LA, Gurnell J, Martinoli A, Tosi G (2002) Interspecific competition between native Eurasian red squirrels and alien grey squirrels: does resource partitioning occur? *Behavioral Ecology and Sociobiology* **52**(4), 332-341.

Wauters LA, Lens L (1995) Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. *Ecology* **76**(8), 2460-2469.

Wauters LA, Lurz PWW, Gurnell J (2000) Interspecific effects of grey squirrels (*Sciurus carolinensis*) on the space use and population demography of red squirrels (*Sciurus vulgaris*) in conifer plantations. *Ecological Research* **15**(3), 271-284.

Wauters LA, Matthysen E, Adriaensen F, Tosi G (2004) Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. *Journal of Animal Ecology* **73**(1), 11-25.

Weisstein EW (2014) 'Standard Error.' Available at: http://mathworld.wolfram.com/StandardError.html Accessed: April 15, 2014.

Wheeler SS, Barker CM, Fang Y, Armijos MV, Carroll BD, Husted S, Johnson WO, Reisen WK (2009) Differential impact of West Nile virus on California birds. *The Condor* **111**(1), 1-20.

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120-S139.

White PCL, Jennings NV, Renwick AR, Barker NHL (2005) Review: questionnaires in ecology: a review of past use and recommendations for best practice. *Journal of Applied Ecology* **42**(3), 421-430.

White T, Lundy M, Montgomery W, Montgomery S, Perkins S, Lawton C, Meehan J, Hayden T, Heckel G, Reid N, Searle J (2012) Range expansion in an invasive small mammal: influence of life-history and habitat quality. *Biological Invasions* **14**(10), 2203-2215.

Williamson MH, Fitter A (1996) The characters of successful invaders. *Biological Conservation* **78**(1,2), 163-170.

With KA (2002) The landscape ecology of invasive spread. *Conservation Biology* **16**(5), 1192-1203.

Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**(7144), 581-584.

Wolf M, Weissing FJ (2010) An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1560), 3959-3968.

Wood DJA, Koprowski JL, Lurz PWW (2007) Tree squirrel introduction: a theoretical approach with population viability analysis. *Journal of Mammalogy* **88**(5), 1271-1279.

Yoder CA, Mayle BA, Furcolow CA, Cowan DP, Fagerstone KA (2011) Feeding of grey squirrels (*Sciurus carolinensis*) with the contraceptive agent DiazaCon™: effect on cholesterol, hematology, and blood chemistry. *Integrative Zoology* **6**(4), 409-419.

Zollner PA (2000) Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology* **15**(6), 523-533.

Appendix 1

Detailed costs by category of the hair-tube survey (Table A), both total and per survey, and the citizen science survey (Table B), total and per week, to detect squirrel presence.

Where appropriate costs are separated by initial outlay or per survey/week.

Table A

Hair-Tube Study	*Initial outlay (€)*	*Price per unit (€)*	*Price per survey (€)*	*Total (€)*
Personnel				
Tube construction	425.00	25.00 hr^{-1}		425.00
Planning		12.50 hr^{-1}	25.00	350.00
Deploy/collect		12.50 hr^{-1} (x2)	400.00	5600.00
Hair analysis		12.50 hr^{-1}	100.00	1400.00
Travel				
Travel to/from site		0.39/km	143.52	2009.28
Equipment				
Tubes	144.65	1.45		144.65
Glue blocks	10.00	0.05		10.00
Wire	45.00			45.00
Adhesive paper	18.20	1.30 $sheet^{-1}$		18.20
Craft glue	4.00			4.00
HistoClear	54.70			54.70
Twine	24.00			24.00
Bait/Consumables				
Plastic bags (2 sizes)	52.49			52.49
Vegetable oil	2.15			2.15
Gelatin	30.91			30.91
Microscope slides	23.27			23.27
Hazelnuts		0.055 $tube^{-1}$	1.65	23.10
Maize		0.01 $tube^{-1}$	0.39	5.46
Peanuts		0.058 $tube^{-1}$	1.74	24.36
Total	834.37		672.30	10246.57

Table B

Citizen Sci. Survey	*Initial outlay (€)*	*Price per unit (€)*	*Price per week (€)*	*Total (€)*
Personnel				
Website design	859.92	30.00 hr^{-1}		859.92
Website mgmt.		30.00 hr^{-1}	4.04	420.00
Data mgmt.		12.50 hr^{-1}	100.00	10400.00
Newspaper publicity	200.00	12.50 hr^{-1}		200.00
Interviews	200.00	12.50 hr^{-1}		200.00
Public presentations	200.00	12.50 hr^{-1}		200.00
Travel				
Poster publicity	448.50	0.39 km^{-1}		448.50
Equipment				
Website hosting		71.00 $year^{-1}$	1.37	142.00
Bait/Consumables				
Poster printing	60.00	0.30 $poster^{-1}$		60.00
Total	1968.42		105.40	12930.42

Appendix 1a

Hair tube site locations and site-specific results

Site	Name	*S. vulgaris*	*S. carolinensis*	*A. sylvaticus*	*R. norvegicusus*	*M. glareolus*	*M. martes*	*M. musculus*	*C. russula*	*M. erminea*	bird
1	Kildanoge	5	0	5	1	0	0	0	0	0	2
2	Glengarra	4	0	5	0	1	0	0	0	0	1
3	Cahir Park	0	1	3	1	0	0	0	0	0	15
4	Gortavoher	1	0	8	1	2	0	0	0	0	12
5	Anglesborough	9	0	2	0	1	0	0	0	0	0
6	Killeen	4	0	5	3	1	1	0	0	0	1
7	Ballyhoura	10	0	5	1	0	0	1	1	0	2
8	Ballydavid	15	0	3	1	0	0	1	0	0	13
9	Carey's Castle	3	0	8	0	1	0	0	0	0	15
10	Tikincor	0	0	11	5	1	0	0	0	0	5
11	Bansha Wood	2	1	10	6	0	0	0	0	1	9
12	Killurney	3	0	1	1	1	0	0	0	0	0
13	Gortarush	6	1	6	0	0	0	0	0	0	12
14	Kilnamack	1	1	4	1	0	2	0	0	6	2

Appendix 2

Calculations of a) annual survival probability, b) standard error of annual survival probability, and c) recapture probability.

a) Annual (50 week) survival probability from estimates of monthly (5 week) survival based on seasons (summer: April – September, winter: October – March)

Winter ϕ = 0.9522903 SE = 0.0148177
Summer ϕ = 0.8345435 SE = 0.0228236

$$Annual\ survival\ =\ (winter\phi)^5(summer\phi)^5\ =\ 0.317023676$$

b) Use of the Delta Method to approximate the SE of annual survival probability

$$var(\gamma) = D\Sigma D^T$$

Where D is the vector of the partial derivative of a function γ with respect to each parameter in turn. Σ is the variance-covariance matrix. D^T is the transpose of D.

First create a vector of the partial derivative of the linear transformation of the function γ with respect to each parameter in turn. Then multiply this by the variance-covariance matrix (MARK will output this and it can be opened as an excel file).

$$var(\gamma) = \begin{bmatrix} \frac{\delta\gamma}{\delta\Phi_1} & \frac{\delta\gamma}{\delta\Phi_2} \end{bmatrix} * \begin{bmatrix} var\Phi_1 & covar\Phi_2\Phi_1 \\ covar\Phi_1\Phi_2 & var\Phi_2 \end{bmatrix} * \begin{bmatrix} \frac{\delta\gamma}{\delta\Phi_1} \\ \frac{\delta\gamma}{\delta\Phi_2} \end{bmatrix}$$

It does not matter what the function γ is because it cancels out as follows:

$$var(\gamma) = [\Phi_2 \quad \Phi_1] * \begin{bmatrix} var\Phi_1 & covar\Phi_2\Phi_1 \\ covar\Phi_1\Phi_2 & var\Phi_2 \end{bmatrix} * \begin{bmatrix} \Phi_2 \\ \Phi_1 \end{bmatrix}$$

Plug in the values:

$$var(\gamma) = [0.8345435 \quad 0.9522903] * \begin{bmatrix} 0.0002195644 & -0.000471727 \\ -0.000471727 & 0.0005209176 \end{bmatrix} * \begin{bmatrix} 0.8345435 \\ 0.9522903 \end{bmatrix}$$

Convert variance to standard error:

$$\sqrt{var(\gamma)} = \sqrt{0.002189352} = 0.046790513 = SE$$

The standard error of an estimate can be defined as the square root of the estimated error variance, as above (Weisstein 2014)

c) Calculation of recapture probability

Estimates of p

p_1 = winter2011-2012(p)	= 0.7233911	SE = 0.0591054
p_2 = summer2012(p)	= 0.7589078	SE = 0.0306088
p_3 = winter2012-2013(p)	= 0.4886857	SE = 0.0401004
p_4 = summer2013(p)	= 0.8792056	SE = 0.0513550

$$2012\ annual\ recapture\ probability = (p_1)^2(p_2)^5(p_3)^3 = 0.015373767$$

Appendix 3

Grey squirrel demographic values extracted from published literature.

Region	Habitat/notes	Method	Location on Frontier	Density (squirrels/ha)	Survival Rate (%)	Breeding Rate (%)	Litter Size/Juvenile Recruitment	Home Range Size (ha)	Body Mass (g)	Source
Ireland	Deciduous	Trapping	F	1.14	31.7±4.7	67.9			580.5±6.8 (F) 551.5±6.7 (M)	This study
Ireland	Mixed	Trapping	F	0.38	31.7±4.7	75			625.6±10.6 (F) 565.8±11.3 (M)	This study
Ireland	Mixed (BP, culled)	Trapping	E	1.7		25.6		0.397-0.413 (F) 0.329-1.704 (M)	607.7 (F) 606.9 (M)	(Lawton 1999; Lawton and Rochford 2007)
Ireland	Deciduous (ard, culled)	Trapping	E	1.83		38.7		0.397-0.413 (F) 0.329-1.704 (M)	630.7 (F) 592.8 (M)	(Lawton 1999; Lawton and Rochford

										2007)
Ireland	Deciduous	Trapping	E	1.76		28.6 (spr) 33.3 (sum)		6.58±3.15 (F) 1.95±0.15 (M)	604.28±10.66 (F) 540.03±11.25 (M)	(O'Teangana 1999)
Ireland	Conifer	Trapping	E	0.95		62.5 (spr) 26.7 (sum)		6.58±3.15 (F) 1.95±0.15 (M)	655.55±24.22 (F) 564.95±30.93 (M)	(O'Teangana 1999)
Ireland	Deciduous	Trapping	E	2.8-6.0	36-52.9 0-46.9 (J)	78-100			510-580 (medians from culls)	(McGoldrick 2011)
Ireland	Deciduous	Trapping	E	1		91			599±20 (F) 567±14 (M)	(Sheehy 2013)
UK	Urban Mixed	Visual Transect	E	1.7						(Kyle 2009)
UK	Semirural Mixed	Visual Transect	E	2.7						(Kyle 2009)
UK	Conifer	Trapping	E						570±51.1 (F) 566±57.9 (M)	(Lurz and Lloyd 2000)
UK	Conifer	Trapping							588	(Bryce *et al.* 2001)
UK	Deciduous	Trapping	E	2.7±0.57	58±6 27-70 (J)		0.69-1.14 (W)	2.94±0.71		(Kenward and Holm 1993)

UK	Deciduous	Trapping	E	8.8	50 (F) 34 (M) 29 (JF) 34(JM)					(Gurnell 1996)
UK	Conifer	Visual Transect	E	0.54-1.88						(Gurnell *et al.* 2004a)
UK	Conifer	Trapping	F	0.92-1.1	67 (F) 50 (M)	70 (spr) 52 (sum)	41% (R)			(Wauters *et al.* 2000)
UK	Deciduous (n=3)	Trapping	E	2.4±0.44	81±4 31±13 (J)	56±7				(Kenward *et al.* 1998)
UK	Conifer (n=3)	Trapping	E	1.64±0.22	50±7 26±11 (J)	57±15				(Kenward *et al.* 1998)
UK	Conifer	Trapping	E	0.8	45-50			0.89		(Kenward and Hodder 1998)
UK	Deciduous	Drey Counts	E	1.7						(Fitzgibbon 1993)
UK	Deciduous (n=30)	Trapping	E	1.6±0.3 0.25±0.07 (J)			1.85±0.38 (W)			(Kenward and Parish 1986)
UK	Deciduous	Trapping	E	0.98*				4.79*	542-659	(Kenward 1985; Kenward and

										Tonkin 1986)
UK	Deciduous	Trapping	E	2.33				1.79		(Kenward 1985)
Italy	Deciduous (year 1)	Trapping	F	1.0	67 (F) 100 (M)	50 (spr) 100 (sum)	2.0 (W) 80-100% (R)	3.7 (F) 4.5 (M) 1.1 (JF) 2.4 (JM)	549±13 509±17 (J)	(Gurnell *et al.* 2001)
Italy	Deciduous, (year 2)	Trapping	F	1.9	57 (F) 40 (M)	86 (spr) 37 (sum)	2.0 (W) 50-67% (R)	3.7 (F) 4.5 (M) 1.1 (JF) 2.4 (JM)	549±13 509±17 (J)	(Gurnell *et al.* 2001)
Italy	Deciduous	Trapping	E					1.80±1.50- 3.69±1.39 (F) 3.73±1.25- 4.52±0.92 (M)		(Wauters *et al.* 2002)
West N. America	Conifer	Trapping	E	2.54±0.4		77			603.7±15.59 (F) 608.6±11.91 (M)	(Hwang and Lariviére 2006)
West N. America	Deciduous/ Mixed	Trapping	E	0.69-0.88			1.5 (W)		562.5 (F) 594.2 (M)	(Robinson and Cowan 1954)
East N. America	Deciduous	Trapping	N					2.39 (F) 3.41 (M)		(Tounzen *et al.* 2012)
East N. America	Deciduous (hunted)	Trapping	N	11.1	52.5 56 (J)		1.53 (W) 41% (R)	1.45		(Mosby 1969)
East N. America	Deciduous (natural)	Trapping	N	14.1	57.6 43 (J)		1.18 (W) 35% (R)	1.45		(Mosby 1969)

East N. America	Deciduous	Trapping	N	1.5*						(Fischer and Holler 1991)
East N. America	Mixed	Trapping	N	1.26*						(Fischer and Holler 1991)
East N. America	Conifer	Trapping	N	0.49*						(Fischer and Holler 1991)
East N. America	Deciduous	Trapping	N	4.4	46.4 35.6 (J)	70.7	3.1±0.4 (N) 1.5 (W)			(Thompson 1978a)
East N. America	Mixed	Visual Transect	N	0.175						(Healy and Welsh 1992)
East N. America	Deciduous (bad year)	Trapping	N		54.04* 0.10* (J)				547.2±42.0 245.0±29.3 (J)	(Koprowski 1991)
East N. America	Deciduous (good year)	Trapping	N		18.8* 36.38* (J)				612.3±54.3 309±39.2 (J)	(Koprowski 1991)
East N. America	Deciduous	Trapping	N		50 (F) 77 (M) 18-42 (JF) 45-50 (JM)					(Gorman and Roland 1989)
East N. America	Deciduous	Removal	N				2.36 (N,spr) 2.69 (N,sum)			(Hibbard 1935)
East N. America	Mixed	Trapping	N	1.26*	52 26 (J)		2.28 (W)			(Barkalow Jr *et al.* 1970)

East N. America	Deciduous	Trapping	N	1.19*						(Bouffard and Hein 1978)
East N. America	Deciduous	Trapping	N					0.49		(Doebel and McGinnes 1974)
East N. America	Deciduous	Trapping	N	1.6-2.5	40-48 23-41(J)		2.68 (N)		570-586	(Longley 1963)
East N. America	Deciduous (hunting present)	Trapping	N	1.1-1.9	15.1-20	68.2 (spr) 53.2 (sum) 21.4 (both)			528.1 (F) 522.6 (M)	(Nixon *et al.* 1967; Nixon and McClain 1969; Nixon *et al.* 1975)
East N. America	Deciduous	Trapping	N	15.7					518.3	(Montgomery *et al.* 1975)
East N. America	Deciduous (Pre clearcut)	Trapping	N	5.19-7.75				2.1		(Nixon *et al.* 1980)
East N. America	Deciduous (Post clearcut)	Trapping	N	3.57-7.22						(Nixon *et al.* 1980)
East N. America	Deciduous	Trapping	N	0.3-1.75**	49.4**		54.9% (R)**			(Brown and Batzli 1985)

East N. America	Deciduous	Trapping	N	0.1-0.3**	36.1**		57.2% (R)**			(Brown and Batzli 1985)

For “Location on Frontier”: F=introduced, on frontier, E=introduced, established population, N=native range.
For “litter size”: N=nestling, W=weaned, R=recruited
All values for adults of both sexes unless defined by J=juvenile, F=female, M=male.
*=mean calculated from values reported, ** = data taken from graphs.